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Responses of bats to clear fell harvesting in Sitka Spruce plantations, and implications for wind turbine installation

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Highlights:
- Keyhole felling for turbine installation is common in upland plantations
- Despite evidence that bats make use of plantations, the impacts of felling are unknown
- We found that bat activity either increased or stayed the same post harvesting
- Species-specific increases in activity were greatest in small/recently felled stands
- Siting wind turbines in conifer plantations may result in increased bat mortality
Abstract

Commercial coniferous plantations are often assumed to be poor habitats for bats. As a result, the impact of forest management practices on bats, such as clear felling, has received little attention, particularly in Europe. However, there is growing evidence from multiple regions that bats do make use of plantation landscapes, and as interest in siting onshore wind turbines in upland conifer plantations grows, there is an urgent need to examine whether felling prior to turbine installation is likely to put foraging bats at risk of collision. In the first study of its kind, we use a “before – after – control - impact” study to explore the short-term impacts of clear fell harvest on bat activity in commercial plantations. Thirty-one mature stands of Sitka Spruce were surveyed using acoustic detectors in three large, upland Sitka Spruce plantations in Britain. Eleven stands were felled between 2013 and 2015, and 26 of the original 31 stands were resurveyed in 2015. The change in total bat activity and species- or genus-specific bat activity was modelled before and after felling occurred at both felled and control stands using generalised linear models. There was no change in overall bat activity at felled sites compared to control sites, but activity of Nyctalus species was 23 times higher following felling. Total Pipistrellus spp. activity doubled at felled sites post-harvesting, although this was mainly driven by increased activity at a few felled sites. When P. pygmaeus and P. pipistrellus were considered separately, activity increased slightly but non-significantly. The size of the felled area influenced activity (for bats overall and Pipistrellus spp.), with 90% higher activity in smaller felled stands (less than 5ha\(^{-1}\)) compared to larger felled stands (greater than 30ha\(^{-1}\)). For P. pipistrellus, activity in felled areas decreased with the duration since harvesting; the greatest activity occurred in stands felled within two months compared to those harvested more than 16 months previously. Higher activity for some groups following felling may occur due to the creation of more edge habitat, which is preferred by both Pipistrellus species we recorded. An increase in activity following the small-scale felling (‘key-holing’) required for the installation of turbines could put foraging bats at risk from collisions with turbines. Further investigation of the influence of both size of clear fell patch, timing of felling and changes in invertebrate abundance due to felling are required to establish the potential risk of key-holing and turbine installation to foraging bats.

1 Introduction:

Large scale clear felling is a widely used form of timber extraction in commercial forests which has been heavily criticised for its perceived impacts, particularly on forest dependent flora and fauna (Borkin and Parsons, 2014; Lindenmayer et al., 2006). However, there is little consistency in the literature about the impacts of clear felling on biodiversity, with responses being highly taxa specific. Felling may negatively affect organisms by isolating populations, decreasing resources, increasing predation or changing climatic conditions (Grindal and Brigham, 1998). For example, forest
specialists may be negatively affected due to increased predation risk from the lack of cover (e.g. arboreal sciurids; Fisher 2005). However, felling may be beneficial for open and edge adapted species, particularly successional species, which respond positively to the changes in vegetation structure and composition caused by harvesting and preferentially use clear-cuts (e.g. some early successional birds; Loeb and O’Keefe, 2011; Oxbrough et al., 2010; Paquet et al., 2006). Eycott et al. (2006) found that plant species richness is 60% lower in stands with full canopy closure and increased in the first few years post-harvest as regeneration occurs. Regeneration may be positive for some invertebrate taxa (Lin et al., 2006), but less so for canopy specialists (Humphrey et al., 2003). Typically, generalist and open specialist species appear to benefit from clear felling, while forest specialist abundance and diversity decreases (Humphrey et al., 2003; Ohsawa and Shimokawa, 2011; Oxbrough et al., 2010). Therefore, while species richness may not necessarily change in response to felling pressure, community composition can be altered.

Many habitat selection studies have found that bats avoid commercial coniferous plantations (Boughey et al., 2011; Jones et al., 2003; Smith and Racey, 2008; Walsh et al., 1996), which is often attributed to low invertebrate density and increased structural complexity, amongst other factors (Haupt et al., 2006; Russo and Jones, 2003; Smith and Racey, 2008). However, often these studies are carried out in areas of extremely low conifer cover (e.g. conifer cover of less than 3%, Davidson-Watts and Jones, 2005; Davidson-Watts et al., 2006) and there is growing evidence that certain bat species are able to make use of intensively managed non-native plantations in landscapes dominated by plantations (Charbonnier et al., 2016; Cistrone et al., 2015; Kirkpatrick et al., 2017; Mortimer, 2006; Russo et al., 2010). While the impacts of logging forests have been investigated for a number of different bat species worldwide (e.g New Zealand: Borkin and Parsons, 2010a, 2010b; USA: Grindal and Brigham, 1998; Australia: Law and Law, 2011), much of the previous work has concentrated primarily on old growth or native forests (Dodd et al., 2012; Grindal and Brigham, 1998; Loeb et al., 2006; Loeb and O’Keefe, 2011; Menzel et al., 2002; Patriquin and Barclay, 2003). The impact of forest management practices in non-native commercial plantations has received far less attention. Research that does exist has focused on the impacts management may have on forest specialist bats which rely on tree roosts for much of their life cycle (Borkin et al., 2011; Borkin and Parsons, 2014). For bat species which are adept at using anthropogenically-disturbed habitats and rely on building roosts rather than tree roosts, commercial coniferous plantations may be a landscape which they can exploit (Kirkpatrick et al., 2017).

Bats with home ranges dominated by plantation forests, are likely to come into contact with felling operations (Borkin and Parsons, 2011). Features such as standing dead wood, snags, tree damage such as double leaders, and peeling bark all form key roosting habitats for bats and other taxa
trees are removed before these features develop due to reaching economic maturity, safety concerns, damage, fire risk or to limit the spread of parasites (Russo et al., 2010). Depending on the plantation system, felling may therefore directly cause direct mortality by removal of a roost that is currently occupied by a bat colony or indirect mortality through impacting reproductive fitness and success as the number of roost trees within a colony home range is reduced (Borkin and Parsons, 2014). Therefore remnant patches of either native or old growth trees may constitute the only available appropriate natural structures for roosts (e.g. Burgar et al., 2015; Lindenmayer and Hobbs, 2004).

Clear felling causes an immediate and substantial change to stand structural complexity, which may benefit foraging success in edge and open adapted bats (Adams, 2012; Elmore et al., 2005; Kirkpatrick et al., 2017). In stands with substantial vegetative clutter, bat activity will be reduced due to constraints on both echolocation and manoeuvrability (Dodd et al., 2012; Morris et al., 2010; Patriquin and Barclay, 2003), and bat activity is likely to increase once clear felling has occurred. Felled stands may support a similar invertebrate abundance compared to mature forest (Dodd et al., 2012; Lacki et al., 2007; Ohsawa, 2005; Oxbrough et al., 2010), particularly in non-native plantations, where felled plantations can be bordered with mature stands, resulting in edge habitat which provides protection from wind and predators (Nicholls and Racey, 2006). Furthermore, invertebrates may accumulate passively along edge habitats due to wind (Law and Law, 2011; Verboom and Spoelstra, 1999). Even when invertebrate availability is lower in felled stands compared to mature stands, bat activity may be higher, suggesting that the structure of the habitat may be more important than prey abundance in determining the spatiotemporal foraging patterns of bats (Adams et al., 2009; Dodd et al., 2012).

Previously, we found evidence of P. pipistrellus and P. pygmaeus making widespread use of three large, predominantly Sitka Spruce (Picea sitchensis) plantations in Scotland and Northern England, with all other species in this geographic range also detected, albeit in low numbers (Kirkpatrick et al., 2017). There was also evidence that Pipistrellus spp. preferentially associated with felled areas (Kirkpatrick et al., 2017), suggesting that some species may increase their foraging activity as a result of harvesting operations. Therefore, providing roost structures are not removed or damaged in the process, felling may result in increased bat activity in commercial plantations.

Knowledge of how bats respond to felling practices is important in understand the potential implications of siting wind turbines in plantations, a practice which has greatly increased in recent years. There is overwhelming evidence to suggest that wind turbines cause both direct and indirect
mortality through barotrauma, collision, and avoidance resulting in changes to habitat use (Voigt and Kingston, 2015), although the extent to which such effects can exert population level impacts is likely to vary greatly between regions. Therefore, a further consideration of this work was to investigate how bat activity changed in response to the size of the clear felled area and the time since felling, and relate this to forest management practices carried out to install wind turbines in commercial plantations.

To our knowledge, the impact of felling on foraging activity of bats in commercial plantations has not been experimentally tested (but see Grindal and Brigham (1998) for a similar study in native forest). In this study we used a before – after – control – impact (BACI) design to quantify the effect of felling on bat activity in the short term (between 1 and 16 months post-felling).

Specifically, we aimed to answer the following questions:

1. What is the short term influence of felling on bat activity and behaviour?
2. What influence does the size of the felled area have on bat activity?
3. How does the age of the clearfell (i.e. time since felling) influence bat activity?

We predict that in the short-term activity is likely to increase post felling with the creation of new edge habitats. Furthermore, we predict that it is likely that the greater increases in activity will occur in the smaller stands compared to the larger stands. Finally, bat activity could be expected to increase as time since felling increases due to the short term change in vegetative structure which may support more invertebrate prey. As we are looking at changes within two years of harvesting, substantial regeneration is unlikely to have occurred which would be likely to reduce bat activity (Law and Law, 2011).

2 Methods:

The study was conducted in three large, intensively managed plantation forests in Central and Southern Scotland, and Northern England (Cowal and Trossachs: 56.188, -4.509; Galloway Forest: 55.117, -4.4728; Kielder Forest: 55.158, -2.442). All three forests were chosen because of their large size (between 30,000 – 114,000 ha), high productivity and predominance of *Picea sitchensis*, which is the most commonly planted and intensively managed coniferous tree species in Europe (Boye and Dietz, 2005). Within each plantation, multiple sites (total n=31) were selected, each with a range of different stand ages including mature stands of harvestable age. Sites were at least 4 km from each other to reduce spatial autocorrelation (Bellamy et al., 2013). Bat activity was surveyed pre- and post-harvesting at a total of 26 mature stands (11 harvested between Autumn 2013 and Spring
2015; 15 control stands which were not felled). Access to the remaining five sites was not possible due to changes in ownership or deterioration of access routes into the plantation area.

2.1 Bat surveying:
Data on pre-harvesting activity was collected in the summer of 2013, and post-harvesting activity in the summer of 2015. Stands were surveyed for a single night, starting 30 minutes after sunset ensuring that recorded individuals would be actively foraging rather than commuting, and continuing for four hours (the length of the shortest night in our study area); surveys were only carried out on dry nights above 8°C and with wind speeds below Beaufort 4. While we recognise that surveying for a single night provides only a snapshot of bat activity, we believe that BACI nature of this experiment provides a robust design with which to address our primary research question. Bat activity was quantified using a SongMeter SM2 Bat+ (Wildlife Acoustics, Inc., Concord, MA). For the initial, pre harvesting surveys, microphones were placed at 1m height, pointed at a 45 degree angle with one at the stand edge (normally adjacent to a track) and another 20 – 40m into the stand interior (see Kirkpatrick et al., 2017 for further details on experimental set up). Data for edge and interior at each site were pooled. Surveying was repeated in the same way following felling, with microphones placed at the exact same locations as previously used. We tried to keep sampling dates as similar as possible between years but this was not always possible due to logistical constraints (date difference between pre and post felling sampling = ± 15 (4 – 33) days).

2.2 Bat call analysis:
We identified all calls manually to species or genus, counting the number of bat passes per night (four hour period; the duration representing the shortest night during the summer at these sites), which was used as a measure of activity. Analyses were conducted for total bat activity and also separately for bats in the genera *Myotis* and *Nyctalus*, and for *Pipistrellus pygmaeus* and *P. pipistrellus*. Bats in the genus *Myotis* have a similar call structure and as such were also identified only to genus. It can be difficult to distinguish between *Nyctalus* calls in cluttered environments (Schnitzler et al., 2003), so again these were only identified to genus. *Pipistrellus* species can be differentiated between due to differences in characteristic call frequency (Fc = frequency of the right-hand end of the flattest part of the call; Russ, 2012) and the call shape, so where possible passes were identified to species level. For passes where it was not possible to assign to either *Pipistrellus* species, we assigned them to genus. We recorded a very small number of *Plecotus auritus* calls but did not carry out further analysis; this species has very quiet calls, so their occurrence is greatly underestimated by using acoustic recordings alone.
2.3 Statistical analysis:

All analyses were carried out in R studio using R version 3.3.1 (R core development team) using the following packages: MASS, lme4, ggplot2. In all models, activity was recorded as passes per four hour period (defined as at least two calls within one second). To assess the effect of felling on foraging activity (question 1), total or species/genus specific activity was modelled with sampling time ("period"; pre/post), treatment ("treatment"; felled/control), and plantation (Cowal and Trossachs, Galloway or Kielder) as fixed factors. To determine if activity changed at harvested sites compared with control sites post-felling, an interaction between pre/post periods and treatment was also included. Models used either a negative binomial (total bat activity, P. pygmaeus, P. pipistrellus, all Pipistrellus and Myotis) or Poisson (Nyctalus) error distribution. Deviance residuals were checked to ensure normality (Crawley, 2007). Two sites with much higher activity for Pipistrellus spp. than all other sites were found to be strongly influencing the results, so analyses for total bat and Pipistrellus activity were carried out both with and without these sites. Both forest and temperature were included in BACI models to account for differences in bat activity due to geographic variation or climatic conditions.

To determine whether the size of the felling area (question 2) or the time elapsed since felling (question 3) influenced bat activity (passes per 4 hour sampling period), we used a generalised linear regression model with a negative binomial error distribution for the 11 harvested sites only. Total bat and Pipistrellus spp. activity (including Pipistrellus spp. calls we were unable to identify to species) and the two Pipistrellus species separately post-felling were response variables, with the size of the felled area (ha) and months since felling included as covariates and plantation ID as a fixed factor. We were unable to model the influence of the size of the felling area or time elapsed since felling for Myotis and Nyctalus due to the low activity we recorded for these genera. One site was found to be heavily influencing the results, so the analysis was carried out both with and without this site.

3 Results:

3.1 Influence of felling on bat activity:

All activity is expressed as bat passes per night. Total bat activity was more than four times higher at treatment compared to control stands after felling had taken place, after controlling for forest and temperature (F= 3.10, p<0.005; Control: Pre 17.4 (95% confidence intervals 12.1 – 25.2), Post 22.4 (15.6 – 32.3); Felled: Pre 22.0 (12.7 – 29.5), Post 96.4 (63.4 – 146.9). However, after removing the two sites with the highest Pipistrellus spp. activity, this difference was no longer significant (F = 0.59,
The impact of felling on bat activity differed between species. *Nyctalus* activity was 23 times higher at the treatment sites post felling (Table 1A, Fig 1E). Overall, *Pipistrellus* activity more than doubled at treatment sites post felling, but only if two sites with high activity levels were included (Table 1A, 1B, Figure 1F, 2D). When both *Pipistrellus* spp. were considered separately, *P. pipistrellus* activity increased slightly but non-significantly post felling, and only if the two outliers were included (Table 1A, Figure 1C, 2C). Although from Figure 1B it appears that *P. pygmaeus* activity increases post harvesting at treatment rather than control sites, this is dependent upon high activity at one site, and once removed there was no significance difference in *P. pygmaeus* activity (Table 1A, B, Figure 2A, 2B). Finally, *Myotis* spp. activity was similar before and after felling at control and treated sites (Table 1A, Fig 1D).

### 3.2 Influence of size of the felled area and time since felling:

Total bat activity, consisting largely of *Pipistrellus* species, declined significantly as the size of the clearfell increased (Table 2A, Figure 3E), and this effect persisted after outliers were removed (Table 2B, Figure 3A). Considering only felled sites, total bat activity was 97% lower in the largest stands (40 ha) compared to smaller stands (3 ha), and similar reductions in activity were seen when *P. pygmaeus* and *P. pipistrellus* were modelled separately (Figures 3B, C, F, G). There was no effect of the time elapsed since felling (which ranged from 1 month – 18 months) on bat activity, with the exception of *P. pipistrellus*, where activity was 90% higher in newly felled stands compared to those felled more than 16 months previously (Table 2A, 2B).

### 4 Discussion

Currently, there is little information available for managers on how management and harvesting operations affect biodiversity in non-native conifer plantations. To our knowledge, this is one of only a few studies to explicitly test the immediate impact of felling on bat activity using a BACI study (e.g. Grindal and Brigham, 1998), and is the only one conducted in commercially managed plantations rather than native forest. While we recognise that sampling for a single night will only provide a snapshot of bat activity and is likely to underestimate the presence or activity of rare species, our primary interest was in assessing differences in activity levels between treatments rather than quantifying species richness per se (Skalak et al., 2012). Furthermore, the potential implications of installing wind turbines in commercial plantations are likely to be most problematic for common species which would be detected by our sampling regime (Skalak et al., 2012).
Across much of Europe, plantation forest systems involve non-native coniferous stands felled before old growth conditions are achieved, rather than the removal of old growth or native forest (FSC, 2012), limiting the applicability of studies conducted in old-growth forests. Here, we found that for some bat species, there was an increase in activity following clear-fell harvesting. However, this was dependent on the size of the clear cut, with higher bat, and particularly Pipistrellus spp., activity at smaller clear cuts compared to larger clear cuts. There is little evidence that felling negatively affects bats through the loss of potential roost trees in this system; both Pipistrellus species preferentially roost in buildings (Altringham et al., 1996), and Sitka Spruce reach economic maturity (<60 years) and are harvested before suitable roost features form, reducing the likelihood of Myotis or Nyctalus breeding colonies being present. This is in contrast to other common plantation tree species such as Pinus nigra or Pinus sylvestris, both of which may form features suitable for bat roosts before reaching economic maturity (Mortimer, 2006). It is likely that Sitka Spruce plantations may be important primarily as foraging habitat, with felling causing little in the way of mortality due to roost loss or reduction in reproductive potential (e.g. Borkin et al., 2011; Borkin and Parsons, 2014).

Radiotracking carried out during 2014 and 2015 found no evidence of lactating female P. pygmaeus roosting in Sitka Spruce, although individuals did use deciduous trees in remnant patches of broadleaf cover as night roosts (Kirkpatrick, 2017).

4.1 Impacts of felling on bat activity

Bat responses to felling were species specific and consistent with predictions from ecomorphology (Aldridge and Rautenbach, 1987; Schnitzler and Kalko, 2001). Open adapted bats, such as Nyctalus spp. which have long thin wings, a high aspect ratio and low-frequency calls, are less manoeuvrable in cluttered conditions, and as expected, increased in activity at felled stands. Similarly, both Pipistrellus species, which are typical edge foragers, had a non-significant trend towards higher activity post-harvest at felled stands compared to control stands, although the extent of the response varied with stand size.

These results contrast with those of Law and Law (2011), who found that bat activity was reduced in native Eucalyptus forests in Tasmania following harvesting, particularly at the stand centre. However, their study was conducted more than five years after felling, during which time substantial changes in stand structure and plant species composition are likely to have occurred. Our study was conducted within two years of felling in a commercially managed system, and as such reflects felled stands rather than stands in which substantial vegetative regrowth has occurred (Law and Law, 2011).
4.3 The influence of the size of the felled area on bat activity

The size of the felled area had a significant, negative impact on bat activity for total bat activity, driven by *P. pygmaeus* and *P. pipistrellus* activity, similar to other studies (Law and Law, 2011; Patriquin and Barclay, 2003). It is possible that the large range in cut block size in this study (2.7 – 39ha) may be responsible for the somewhat equivocal species-specific responses to felling as this is considerably greater than in previous studies (e.g. 0.5 - 1.5ha; Grindal and Brigham, 1998), who found no effect of the size of felled area on bat activity. However, as this study and others have shown, activity is lower in larger felled or open stands, possibly in response to increased perceived predation risk and exposure to adverse microclimatic conditions which impact invertebrate populations (Baker et al., 2013; Grindal and Brigham, 1998). Therefore, for large cut block sizes, the increase in bat activity due to more edge habitat availability and easier access to invertebrate prey (Law and Law, 2011) may not compensate for the increased perceived predation risk (Baker et al., 2013). Clear fell sizes in this study were more representative of current clear fell forestry practices (in countries where clearfelling is practiced as the method of timber extraction) compared to those surveyed by Grindal and Brigham (1998). Again, further comparisons of both felling techniques and extent would be necessary to fully understand the impacts of felling in a commercial forestry context on bat populations.

4.2 Changes in bat activity in relation to time since felling

The change in structural complexity is likely to be driving the change in bat activity we see here, and may be more important in driving bat activity than invertebrate availability (Dodd et al., 2012; Morris et al., 2010). Physical clutter may impede flight efficiency and be harder to negotiate as dense vegetation will result in increased acoustic clutter (Jung et al., 2012; Morris et al., 2010; Patriquin and Barclay, 2003). We did not measure invertebrate abundance before and after felling in this study, and it is also possible that increased ground disturbance, prevalence of deadwood and stagnant groundwater that remains immediately after clear felling results in a short-lived but substantial increase in Nematoceran Diptera abundance (Blackwell et al., 1994), providing an ephemeral food source which bats are able to exploit (Fukui et al., 2006). Therefore freshly felled areas in Sitka Spruce plantations may represent a patchy and ephemeral food resource in the landscape, with minimal physical and acoustic clutter, which is thereby easier to negotiate and hunt in (Patriquin and Barclay, 2003; Pauli et al., 2015). Similarly, Borkin and Parsons, (2014) hypothesised that the reduced home range of *Chalinobus tuberculatus* in exotic pine plantations in Australia partially reflected an increase in potential foraging areas near roost sites post harvesting.

*Pipistrellus pipistrellus* activity decreased as time since felling increased, but *P. pygmaeus* and total bat activity was unaffected. Previous studies have found that the two closely related and
morphologically similar *Pipistrellus* species (*P. pipistrellus* and *P. pygmaeus*), whilst similar in foraging ecology, have habitat and dietary differences (Barlow, 1997; Davidson-Watts et al., 2006; Nicholls and Racey, 2006). Both species were commonly recorded in the three Sitka Spruce plantations surveyed as part of this study, and have previously been found to preferentially forage at felled stands, with activity declining in response to stand age and density (Kirkpatrick et al., 2017). Therefore, it is likely that the increase in bat activity post felling will not continue as stand replanting or regeneration occurs.

**4.4 Implications for wind turbine installation:**

This work has implications for our understanding of how habitat management prior to installing turbines may influence bat activity in plantations. Typically, small areas are felled and kept clear of regenerating vegetation around the turbine site (50m beyond turbine blade tip, Anon., 2015) and access roads are constructed into newly felled areas. Roads are important flyways for some bat species, allowing access into different plantation areas (Grindal and Brigham, 1998; Hein et al., 2009; Law and Chidel, 2002) and may potentially guide bats towards newly installed turbines, particularly *Nyctalus* and *P. pipistrellus*. This may create a patchwork of attractive foraging patches within which turbines have been installed, acting as an ecological trap (Tscharntke et al., 2012), particularly as low structural clutter is maintained in these areas. Since it is assumed that bat activity in upland plantations is low, there are currently no requirements for monitoring post felling and post construction and no guidance on the potential impacts on bats (Mathews et al., 2016). Results from this thesis suggest that some bat species could be at far greater risk from the installation wind turbines in commercial plantations than previously thought. Further investigation of both short and long term responses of bats to keyholing is an urgent priority, particularly for *Nyctalus* species (Mathews et al., 2016).

**4.5 Conclusions**

This study is the first of its kind to investigate the impact of felling on bats in Sitka Spruce plantations and demonstrates not only that upland commercial coniferous plantations are not devoid of bats, but that there is an urgent need for further studies, especially in light of changing land use in upland plantations. We found some evidence that activity of particular species increased, especially in small stands that have been recently felled. Installing wind turbines in upland plantations after keyhole harvesting could therefore have implications for bat activity and mortality.

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### Tables

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<th>Model A (with outliers)</th>
<th>(Intercept)</th>
<th>Treatment (Felled)</th>
<th>Activity: (Post felling)</th>
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<th>Galloway</th>
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<td>0.34 ± 0.41</td>
<td><strong>1.16 ± 0.61</strong></td>
<td><strong>0.26 ± 0.10</strong></td>
<td><strong>-2.36 ± 0.49</strong></td>
<td>-0.49 ± 0.45</td>
<td>0.44</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model B (without outliers)</th>
<th>(Intercept)</th>
<th>Treatment (Felled)</th>
<th>Activity: (Post felling)</th>
<th>Treatment * activity</th>
<th>Temperature</th>
<th>Galloway</th>
<th>Kielder</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>All bat activity</td>
<td>0.74 ± 0.84</td>
<td>0.09 ± 0.27</td>
<td>0.18 ± 0.25</td>
<td>0.23 ± 0.38</td>
<td>0.23 ± 0.06</td>
<td><strong>-1.81 ± 0.29</strong></td>
<td>-0.63 ± 0.27</td>
<td>0.10</td>
</tr>
<tr>
<td><em>P. pygmaeus</em></td>
<td>2.18 ± 1.51</td>
<td>-0.25 ± 0.50</td>
<td>0.32 ± 0.44</td>
<td>0.24 ± 0.70</td>
<td>0.17 ± 0.11</td>
<td><strong>-1.62 ± 0.52</strong></td>
<td>-0.93 ± 0.49</td>
<td>0.26</td>
</tr>
<tr>
<td><em>P. pipistrellus</em></td>
<td>-1.55 ± 1.46</td>
<td>0.58 ± 0.46</td>
<td>0.47 ± 0.42</td>
<td>-0.59 ± 0.65</td>
<td><strong>0.31 ± 0.10</strong></td>
<td><strong>-2.17 ± 0.50</strong></td>
<td>0.51 ± 0.44</td>
<td>0.49</td>
</tr>
<tr>
<td>All <em>pipistrellus</em> activity</td>
<td>1.54 ± 1.29</td>
<td>0.18 ± 0.43</td>
<td>0.25 ± 0.38</td>
<td>0.22 ± 0.60</td>
<td><strong>0.25 ± 0.09</strong></td>
<td><strong>-2.04 ± 0.45</strong></td>
<td>-0.72 ± 0.42</td>
<td>0.40</td>
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</table>

Table 1: Change in bat activity at control and felled sites after harvesting occurred. Presented are model estimates plus standard error for activity per night, including outliers (A) and excluding outliers (B). Parameters with a significant effect are outlined in bold. Models are presented both with (A, n = 26) and without (B, n = 24) two outlying sites.
<table>
<thead>
<tr>
<th>Model</th>
<th>Term</th>
<th>A Estimate ± std error (with outliers)</th>
<th>F-statistic</th>
<th>p value</th>
<th>R2</th>
<th>B Estimate ± std error (without outliers)</th>
<th>F-statistic</th>
<th>p value</th>
<th>R2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total bat activity</td>
<td>(Intercept)</td>
<td>2.55 ± 1.02</td>
<td>2.50</td>
<td>0.01</td>
<td></td>
<td>2.08 ± 1.04</td>
<td>2.00</td>
<td>0.05</td>
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<tr>
<td></td>
<td>Size of felled area</td>
<td>-0.10 ± 0.02</td>
<td>-4.57</td>
<td>&lt;0.001</td>
<td></td>
<td>-0.09 ± 0.03</td>
<td>-3.46</td>
<td>&lt;0.001</td>
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<tr>
<td></td>
<td>Months since felling</td>
<td>-0.04 ± 0.04</td>
<td>-0.99</td>
<td>0.32</td>
<td>0.83</td>
<td>-0.01 ± 0.04</td>
<td>-0.31</td>
<td>0.76</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>Galloway</td>
<td>3.34 ± 0.97</td>
<td>3.46</td>
<td>&lt;0.001</td>
<td></td>
<td>3.30 ± 0.96</td>
<td>3.42</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td></td>
<td>Kielder</td>
<td>5.38 ± 1.05</td>
<td>5.13</td>
<td>&lt;0.001</td>
<td></td>
<td>5.08 ± 1.09</td>
<td>4.65</td>
<td>&lt;0.001</td>
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<tr>
<td>Pipistrellus pygmaeus</td>
<td>(Intercept)</td>
<td>2.16 ± 1.34</td>
<td>1.62</td>
<td>0.11</td>
<td></td>
<td>1.82 ± 1.43</td>
<td>1.28</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size of felled area</td>
<td>-0.11 ± 0.03</td>
<td>-3.53</td>
<td>&lt;0.001</td>
<td></td>
<td>-0.10 ± 0.04</td>
<td>-2.71</td>
<td>0.01</td>
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<td></td>
<td>Months since felling</td>
<td>-0.03 ± 0.06</td>
<td>-0.55</td>
<td>0.58</td>
<td>0.68</td>
<td>-0.01 ± 0.06</td>
<td>-0.18</td>
<td>0.86</td>
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<tr>
<td></td>
<td>Galloway</td>
<td>2.96 ± 1.26</td>
<td>2.34</td>
<td>0.02</td>
<td></td>
<td>2.94 ± 1.31</td>
<td>2.25</td>
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<tr>
<td></td>
<td>Kielder</td>
<td>4.77 ± 1.38</td>
<td>3.45</td>
<td>&lt;0.001</td>
<td></td>
<td>4.57 ± 1.50</td>
<td>3.05</td>
<td>0.002</td>
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<tr>
<td>Pipistrellus pipistrellus</td>
<td>(Intercept)</td>
<td>2.40 ± 1.45</td>
<td>1.65</td>
<td>0.09</td>
<td></td>
<td>2.10 ± 1.52</td>
<td>1.38</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size of felled area</td>
<td>-0.09 ± 0.03</td>
<td>-3.20</td>
<td>0.001</td>
<td></td>
<td>-0.08 ± 0.03</td>
<td>-2.41</td>
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<tr>
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<td>Months since felling</td>
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<td>-2.64</td>
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<td>0.85</td>
<td>-0.12 ± 0.06</td>
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<td></td>
<td>Galloway</td>
<td>1.59 ± 1.42</td>
<td>1.12</td>
<td>0.26</td>
<td></td>
<td>1.58 ± 1.45</td>
<td>1.09</td>
<td>0.28</td>
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<tr>
<td></td>
<td>Kielder</td>
<td>4.99 ± 1.48</td>
<td>3.38</td>
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<td>4.82 ± 1.56</td>
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</tr>
<tr>
<td>Pipistrellus spp.</td>
<td>(Intercept)</td>
<td>2.62 ± 1.12</td>
<td>2.34</td>
<td>0.02</td>
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<td>2.20 ± 1.17</td>
<td>1.88</td>
<td>0.06</td>
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<tr>
<td></td>
<td>Size of felled area</td>
<td>-0.11 ± 0.03</td>
<td>-4.23</td>
<td>&lt;0.001</td>
<td></td>
<td>-0.09 ± 0.03</td>
<td>-3.20</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Months since felling</td>
<td>-0.04 ± 0.05</td>
<td>-0.94</td>
<td>0.34</td>
<td>0.80</td>
<td>-0.02 ± 0.05</td>
<td>-0.39</td>
<td>0.69</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>Galloway</td>
<td>3.15 ± 1.06</td>
<td>2.97</td>
<td>0.003</td>
<td></td>
<td>3.11 ± 1.08</td>
<td>2.90</td>
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<tr>
<td></td>
<td>Kielder</td>
<td>5.38 ± 1.15</td>
<td>4.67</td>
<td>&lt;0.001</td>
<td></td>
<td>5.12 ± 1.23</td>
<td>4.17</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

*Table 2: Change in total bat activity and *P. pygmaeus* / *P. pipistrellus* activity felled sites after felling occurred including the size of felled area and time elapsed since felling in the models. Model estimates plus standard error are presented for activity per four hour sampling period, and are presented both with (A) and without (B) two sites with high activity levels.*
Figure 1: Change in bat activity at control and felled sites before and after harvesting occurs for total and species / genus specific activity. Outlying sites are included (n = 26). Coloured dots depict raw data on bat activity, black dot shows model predicted activity and error bars show 95% confidence intervals.
Figure 2 Change in bat activity at control and felled sites before and after harvesting occurs for total and species/genus specific activity. Outlying sites are excluded (n = 24). Coloured dots depict raw data on bat activity, black dot shows model predicted activity and error bars show 95% confidence intervals.
Figure 3: Change in total, P. pygmaeus, P. pipistrellus and all Pipistrellus activity in response to felled stand area (n = 11). Black dots are raw data, the solid black line is the model prediction for change in activity, the dashed lines are the 95% confidence intervals. Graphs A – D include one site with very high activity (n = 11), graphs E – H exclude outlier (n = 10).