Abstract

Context: Determining an area’s biodiversity is essential for making targeted conservation decisions. Undertaking surveys to confirm species presence or to estimate population sizes can be difficult, particularly for elusive species. Bats are able to detect and avoid traps making it difficult to quantify abundance. Although acoustic surveys using bat detectors are often used as a surrogate for relative abundance, the implicit assumption that activity levels will correlate with abundance is rarely tested.

Aims: We assessed the effectiveness of surveying techniques (i.e. trapping and acoustic monitoring) for detecting species presence and tested the strength of collinearity between methods. In addition, we tested whether the use an acoustic lure (a bat call synthesiser) increased bat capture rate and therefore species detectability.

Methods: Surveying was carried out over three years in central Scotland (UK), in 68 woodlands within predominantly agricultural or urban landscapes.

Key results: There was a significant positive relationship between bat activity recorded on ultrasonic detectors and the number of individuals captured for *Pipistrellus pygmaeus* and *P. pipistrellus*. Acoustic monitoring was more effective than trapping at determining species presence, however to ensure rarer or quiet species are recorded a complementary approach is required. Broadcasting four different types of echolocation call resulted in a 2 to 12 fold increase in trapping success across four species of insectivorous bat found in the
study region. Trapping success was dependent on the type of echolocation call that was broadcast. There was no effect of sex or age on trapping success; however, whilst lure effectiveness remained unchanged for female *P. pygmaeus*, there was a marked increase in the number of males captured using the lure throughout the summer (May to September).

**Conclusions:** In this paper we demonstrate a variety of ways to increase surveying efficiency which can maximise the knowledge of an area’s species richness, minimise wildlife disturbance, and enhance surveying effectiveness.

**Implications:** Increasing surveying efficiency can improve the accuracy of targeted conservation decisions.

**Additional keywords:** acoustic lure, acoustic survey, bat community, capture methods, microchiroptera, surveying efficiency, trapping
Introduction

Obtaining accurate quantitative information on the species richness of an area is difficult, yet it is essential to identify highly biodiverse areas which should be prioritised for conservation (Brooks *et al.* 2006). Species can remain undetected despite extensive surveying while presence records can be spatially biased towards localities that are easier to survey or are more frequented by recorders (Rondinini *et al.* 2006). Estimates of species’ frequency of occurrence or relative abundance are also often used as indices of species persistence to gain a better understanding of how species use habitats (Araújo and Williams 2000). Abundance has been used to form area-based priority-setting criteria for a range of taxa (Gauthier *et al.* 2010). However assessing abundance for rare or elusive species involves considerably more uncertainty and failure to detect species within an area may influence future planning decisions and leave sites vulnerable to habitat loss. Many species of European bat have undergone population declines in the past few decades due to habitat loss and degradation, a consequence of pressure on resources from increasing human populations (Mickleburgh *et al.* 2002). Bats are becoming of increasing importance as bioindicators, therefore gaining accurate estimates of bat population sizes is critical to quantify the extent of these declines (Jones *et al.* 2009). The size of bat populations can be estimated by counting individuals emerging from summer roosts (Jones *et al.*1996) or in hibernacula (O’Shea *et al.*2003), however roosts are often difficult to find and inaccessible. Acoustic surveys using bat detectors are widely used in studies to determine species presence and quantify activity of foraging bats (e.g. Roche *et al.* 2011; Fuentes-Montemeyer...
et al. 2012). However, call intensity varies between species; gleaning species such as *Plecotus* spp. emit calls of short duration, high frequency, and low intensity which may not be detected by acoustic surveys (Waters and Jones 1995). In cluttered habitats, such as woodland, bats emit quieter echolocation calls, which can reduce detection rate and make species identification from ultrasonic recordings more difficult (Russ 1999; Schnitzler and Kalko 2001). Therefore, it is often necessary to confirm species presence within an area by capturing and examining individuals in the hand.

Mist netting and harp trapping are two of the most common methods used to capture bats (O’Farrell and Gannon 1999). However, as with acoustic surveys, inherent biases exist within these sampling techniques including interspecies differences in capture rates (Berry et al. 2004), avoidance-learning behaviour in bats (Larsen et al. 2007), and ambient light levels altering net detectability (Lang et al. 2004). Habitat characteristics can also determine capture rates; trapping is most effective in locations with dense vegetation containing discrete flyways (Duffy et al. 2000; Hourigan et al. 2008). However, some species, such as *Myotis bechsteinii*, rarely use tracks or rides which would therefore decrease their capture rate when surveying within woodland habitat (Hill and Greenaway 2005). Additionally, trapping requires specialist skills, and can cause stress to the animals (Flaquer et al. 2007).

A complementary approach, using a combination of acoustic surveys and trapping techniques, is often found to maximise detection efficiency (Duffy et al. 2000; MacSwiney et al. 2008; Meyer et al. 2011), yet is not always practical due to limitations in expertise, expense, and time requirements (Hourigan et al. 2008). Therefore a number of previous studies have used measurements of bat activity assessed by acoustic monitoring as a surrogate for relative abundance (e.g. Kalko et al. 2008; Razgour et al. 2011; Berthinussen
and Altringham 2012), however to our knowledge this relationship has not been explicitly tested.

Broadcasting natural or synthetic auditory stimuli has been used to increase detection rates by provoking a response that makes individuals more easily detectable. Such “playback” calls have been used to estimate population sizes in a range of amphibian, avian, and mammalian species including *Bufo marinus* (Schwarzkopf and Alford 2007), *Loxia scotica* (Summers and Buckland 2011), and *Panthera leo* (Brink et al. 2012). Behavioural studies have demonstrated that the broadcasting of bat feeding buzzes and social calls can attract both conspecific and heterospecific bats (Russ et al. 1998; Wilkinson and Boughman 1998); this led to the development of an acoustic lure, the Sussex AutoBat (Hill and Greenaway 2005). Field testing found that the capture rate of different bat species, including the rare *M. bechsteinii*, increased with the use of an acoustic lure (Hill and Greenaway 2005; Goiti et al. 2007; Hill and Greenaway 2008), but the extent to which this lure enhances capture rates in comparison to traditional trapping techniques has not, to our knowledge, been systematically tested.

Here, we quantify and compare the effectiveness of traditional surveying methods (acoustic surveys, mist netting and harp trapping) and novel techniques (mist netting and harp trapping with the addition of an acoustic lure), with the aim of informing future surveys for insectivorous temperate bat species. We address five specific questions:

1. Is bat activity, as measured by acoustic surveys, a good surrogate for relative bat abundance?

2. Which surveying method (acoustic surveys or trapping) is most effective at determining species presence within temperate woodland?
3. To what extent does an acoustic lure enhance capture rate in comparison to traditional trapping techniques?

4. Does the type of synthesised bat call broadcast determine capture rate?

5. What is the effect of sex, age, and seasonality on trapping success with an acoustic lure?

Materials and methods

Ordinance Survey digital maps (EDINA Digimap Ordnance Survey Service) were used to select 68 broadleaved and mixed woodland patches of different size (0.1 – 30 ha) and shape (ranging from compact to complex) within central Scotland, UK (Appendix A). This region comprises an intensely developed and densely populated landscape which is dominated by agriculture, large conurbations, coniferous plantations, and fragmented patches of semi-natural habitat including broadleaved woodland. Each woodland was surveyed once during the summers of 2009 (June to August, 20 sites), 2010 (May to July, 14 sites), and 2011 (May to August, 34 sites). Surveying was conducted in dry weather, when the temperature remained ≥ 8 °C throughout the surveying period, and wind speed ≤ 4 on the Beaufort scale. Surveying commenced 30-45 minutes after sunset and continued for the following four hours, the shortest period between sunset and sunrise in this area. A combination of acoustic surveys and trapping was used to determine species presence, relative abundance and activity within each woodland patch.

An estimate of relative abundance was determined by placing an Austbat harp trap (2.4 x 1.8 m) and three Ecotone mist nets (2.4 x 6 m each) within each woodland. Traps were placed ≥ 20 m from the woodland edge, ≥ 40 m from each other and positioned to avoid paths and obvious flyways (i.e. rides and trails). An acoustic lure (The Autobat, Sussex
University) was positioned alongside a trap and moved between traps every 30 minutes for the duration of surveying (Hill and Greenway 2005). Preliminary testing using a frequency division bat detector indicated that the sound emitted by the acoustic lure was detectable from a maximum of 20 m away, although it is likely that bats can hear them from a greater distance (i.e. Murphy 2012). Four different synthesised bat call types were played (Pipistrellus sp. mix, Myotis sp. mix, Nyctalus leisleri, and M. nattereri), which are known to attract a variety of bat species (Greenaway pers. comm.). Call sequences were switched every 15 minutes and played in the same sequence each night. Traps were checked every 15 minutes to extract any captured bats, which were then identified to species, aged, sexed, measured, weighed and marked temporarily by fur clipping. All procedures were preapproved by the University of Stirling ethical review committee and all bats were caught under Scottish Natural Heritage Scientific License.

Bat activity was quantified using a frequency division bat detector (Anabat SD1, Titley Electronics) fixed on a 1 m high pole with the microphone pointing upwards. The detector was positioned adjacent to the centre of the trap (< 1 m away) and rotated between traps every 30 minutes. The sequence of rotation ensured the detector did not record at the same net as the acoustic lure was positioned. All bat recordings were analysed using Analook W (Corben 2006). One bat pass was defined as a continuous sequence of at least two echolocation calls from a passing bat (Walsh & Harris 1996). All nine species of four bat genera present within the study area (Myotis, Nyctalus, Pipistrellus, and Plecotus) can be identified from detector recordings based upon the search-phase of their echolocation call (Russ 1999). However, it can often be difficult to distinguish between Myotis species due to similarities in call structure, particularly within cluttered environments (Schnitzler and Kalko...
As a consequence, recordings of *Myotis* species known to be present in the area (*M. daubentonii*, *M. mystacinus*, and *M. nattereri*) were grouped together as *Myotis* sp. The three *Pipistrellus* species in this area (*P. pipistrellus*, *P. pygmaeus* and *P. nathusii*) can be determined by the characteristic frequency (Fc = the frequency at the right hand end of the flattest portion of a call; Corben 2006) of their search-phase echolocation calls. Bat passes with a Fc of between 49 and 51 kHz were classed as unknown *Pipistrellus* sp..

Statistical analyses were conducted using the statistics package R version 2.14 (R Core Team 2012) run within the R Studio interface (R Studio 2012) and using the package ggplot2 (Wickham 2009). Total captures per site was converted to captures per hour per site (with/without the acoustic lure) as the lure was only operating at one of the four traps at a time within each site. Total bat passes per site was converted to passes per hour. We performed a series of linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis* sp. to determine whether an association exists between bat capture rate and bat activity and if it changes through the season. Bat captures per hour per site was used as the response variable for each species / genus. Bat activity, date and the interaction between them were included as predictor variables in each of the models. Each model was fitted with a Gaussian distribution and if required the capture and activity rates were logged to achieve normality. Non-significant interactions or variables were removed from the model using a step-wise method whereby explanatory variables were dropped or retrained using $P \leq 0.05$ as a threshold. Model validation was conducted by the examination of residuals (Zuur et al. 2009). To determine how the effectiveness of each surveying strategy varies between species we compared the number of woodlands in which species presence was confirmed by either trapping (with and without the lure), acoustic surveys, or both methods combined.
A Mann Whitney U-test was used to determine if the number of species detected per site differed between surveying method. A two-sided Wilcoxon paired test was used to assess trapping success with and without the acoustic lure for each species / genus. The relative effectiveness of the four different synthesised bat call types broadcast by the acoustic lure was tested using a chi-square test. To determine whether trapping success with and without the acoustic lure varied between sex or age (adult / juvenile), two-sided Wilcoxon paired tests were conducted on *P. pygmaeus* only as there were insufficient numbers of other species captured. We also tested whether the effect of the lure on male and female *P. pygmaeus* changed with date throughout the active season using linear regressions for males and females separately. Regression models were validated by visual examination of residuals (Crawley 2007).

**Results**

**Bat activity and abundance**

We captured a total of 376 bats in 64 of the 68 woodlands, and recorded a total of 16,121 usable bat passes (i.e. identifiable to species/*Myotis* sp. level), with activity recorded in 66 of the 68 woodlands. We identified five species/genera by acoustic surveys; *P. pygmaeus*, *P. pipistrellus*, *P. nathusii*, *P. auritus* and *Myotis* spp. Six species were identified by trapping; *P. pygmaeus*, *P. pipistrellus*, *P. auritus*, *M. nattereri*, *M. daubentonii* and *M. mystacinus*. With the exception of *M. mystacinus*, all species were captured in traps both with and without the use of an acoustic lure (Table 1). Abundance of *M. mystacinus* and *M. daubentonii* was insufficient to conduct analyses at species level; therefore abundance of all *Myotis* species was grouped together and analysed at the genus level. *P. nathusii* was only recorded in one site and therefore excluded from further analysis.
Correspondence between acoustic surveys and capture rates

Both bat activity and date were significant predictors of *P. pygmaeus* abundance (captures per hour) per woodland. Bat activity was a marginally significant predictor of *P. pipistrellus* capture rate however date was not a significant predictor. Neither activity nor date was a significant predictor of *Myotis* sp. capture rate (Table 2; Fig 1). *P. auritus* was not included in this analysis due to its presence in relatively few sites (Table 1).

Effectiveness of surveying methods at determining species presence

On average, 1 more species was detected by acoustic surveying than by trapping per site (n=64, U =2983, p = 0.001). Of the 68 survey sites, acoustic surveying recorded more species in 41 of the sites, trapping detected more species in two sites, while both methods recorded the same species in 19 sites. *P. pipistrellus* showed the greatest difference in detection between methods with acoustic surveys detecting this species at an additional 38 sites compared to trapping (Table 1). Trapping added only one additional site to those where *P. pipistrellus* presence had already been confirmed through acoustic surveys (Table 1). In contrast, for *P. auritus*, trapping increased the number of sites at which it was detected by seven (out of a total 16) woodlands.

Effect of an acoustic lure on capture rate

The acoustic lure significantly increased capture rates for all species. *P. pygmaeus* showed the strongest response (n= 56, v=1593, p = 0.001) with a 12-fold increase in individuals
caught using the acoustic lure. Likewise, 7.5x more *P. pipistrellus* were caught when the lure was adjacent to a trap (n= 15, v= 117, p =0.001). The acoustic lure increased the capture rate of both *M. nattereri* (n=17, v=127, p=0.017) and *P. auritus* (n=9, v=39, p=0.055) by 2.25x and 3.5x respectively (Fig 2).

Effect of broadcasting different types of synthesised bat call on capture rate

There were significant differences in the effectiveness of the type of call sequences broadcast by the lure in attracting *P. pygmaeus* ($\chi^2 = 63.91$, d.f. = 3, p=0.001), *P. pipistrellus* ($\chi^2 = 8.67$, d.f. = 3, p = 0.034), and *P. auritus* ($\chi^2 = 7.86$, d.f. = 3, p=0.049) (Fig 3). *P. pipistrellus* and *P. pygmaeus* responded more strongly than expected by chance to synthesised calls of *N. leisleri*, *Myotis* sp. mix, and *Pipistrellus* sp. playback calls, while very few were captured with synthesised calls of *M. nattereri*. In contrast, *P. auritus* was not trapped when *M. nattereri* or *Pipistrellus* sp. playback calls were broadcast but showed a strong response to *Myotis* sp. mix and *N. leisleri* calls. There was a marginal difference in the effectiveness of each of the call sequences in attracting *M. nattereri* ($\chi^2 =6.6$, d.f. = 3, p=0.086) with the calls of *N. leisleri* instigating the greatest response.

Effect of sex, age, and seasonality on trapping success of *P. pygmaeus* with an acoustic lure

The acoustic lure significantly increased the capture rate of both male (n= 51, v=1316, p = 0.001), and female (n= 39, v=702, p = 0.001) *P. pygmaeus*. Broadcasting synthesised bat calls also significantly increased the capture rate of both juvenile (n= 23, v=273, p = 0.001), and adult (n= 54, v=1482, p = 0.002) *P. pygmaeus*. The effectiveness of the acoustic lure for
female *P. pygmaeus* did not vary across the active season ($F_{1,55} = 1.04, p = 0.321$), but males responded more strongly to the lure later in the summer than in the spring ($F_{1,48} = 20.3, p = 0.001, r^2 = 0.3$; Fig 4).

Insert Figure 4

**Discussion**

*Bat activity and abundance*

Occurrence data is often used for comparisons of biodiversity between areas; however it can underrepresent species with low detection rates (e.g. gleaning species) or underestimate diversity in situations of insufficient sampling effort (Gu and Swihart 2004). Achieving satisfactory species inventories through field surveys can be time consuming and costly. The accuracy of diversity estimates improves, and the potential to detect previously unseen taxa increases as sampling effort increases (McCabe 2012). In this study we have shown that the use of two complementary techniques, acoustic surveys and trapping, reduces the potential of misrepresenting the total species richness of an area. In addition, we have shown that for certain species, and in circumstances where relative abundance is required for use as an index of species persistence (Araújo and Williams 2000), or for understanding community structure (Magurran and Henderson 2003), acoustic surveying can be used as a surrogate for relative abundance.

*Using acoustic surveys as a surrogate for relative bat abundance*

Acoustic surveys are widely used in field studies to act as an index of relative abundance however the relationship between these two indices is rarely tested (e.g. Kalko *et al*. 2008). Trapping can be a costly and time consuming process requiring expertise whilst acoustic
surveys are non-intrusive and comparatively simple. Here, we showed that, in the case of P. pygmaeus and P. pipistrellus, activity levels vary positively with relative abundance and could be used a surrogate for abundance to increase surveying efficiency. This provides additional support that surveys monitoring population change over time (e.g. Bat Conservation Trust’s Field Survey, part of a suite of surveys in the National Bat Monitoring Programme (Bat Conservation Trust 2013)) are reflecting relative changes in bat populations despite only using acoustic surveys. A significant relationship was found between P. pygmaeus capture rate and date which may reflect a heightened response to the acoustic lure with date as discussed below. There was no significant relationship between Myotis sp. activity and capture rate. This is unsurprising given that each species within this group is likely to have varying levels of detection by acoustic surveys (e.g. flight height) and capture rates (e.g. differing responses to an acoustic lure). Combining the data into a larger species group will therefore mask any species specific relationship between activity and capture rate from being observed.

Effectiveness of surveying methods at determining species presence

Although using multiple surveying methods can maximise species detection efficiency (MacSwiney et al. 2008; Meyer et al. 2011), it is often impractical. This study demonstrates that a complementary approach can be unnecessary if the aim of surveying is to determine the presence of conspicuous species within a habitat. For instance, we found only a marginal benefit of undertaking both acoustic surveys and trapping for P. pipistrellus and P. pygmaeus. Given that bat detectors are cost effective, can be automated to run for long time periods, and are non-intrusive (Hourigan et al. 2008), acoustic surveys alone are a satisfactory method for surveys which focus on a specific conspicuous species. In
comparison, accurately determining bat community composition or the presence of quiet species such as P. auritus might require a complementary approach. This supports the work by Flaquer et al. (2007) who found that rarer species are often only detected by one method, which suggests they could be easily overlooked if only one sampling technique is used. Additionally, trapping can provide confirmation to species level for every individual captured, in contrast to acoustic surveys which in some cases can be problematic in achieving this level of accuracy due to call similarities between species (Walters et al. 2012).

In addition, the effectiveness of each surveying method may differ depending upon the habitat type that they are used in (e.g. between open and closed habitat).

Effect of an acoustic lure on capture rate

The acoustic lure greatly increased bat capture rate, with between a 2 and 12 fold increase in trapping success across species. Bats are known to respond to conspecific and heterospecific calls (Fenton 2003, Dechmann et al. 2009; Knörnschild et al. 2012) and the acoustic lure appeared to invoke a similar response to the synthesised calls that were played. Although we demonstrated the effectiveness of the lure in increasing bat capture rate, the ecological mechanism by which it works is currently unknown. A response may have occurred due to bats eavesdropping on surrounding calls to locate food sources (Gillam 2007), or acting aggressively to a perceived competitor (Hill and Greenway 2005). Additionally it is plausible that the lure may be impairing the bats’ ability to echolocate thereby masking the position or presence of the trap. Mist nets and harp traps are conspicuous acoustic targets to bats (Berry et al. 2004); detection rates may therefore be reduced by an increased external sensory input. Bats exhibit high rates of trap avoidance (Larsen et al. 2007), which the use of an acoustic lure appears to reduce. It is likely that we
have underestimated the effectiveness of the acoustic lure given that some bats respond to
the lure but do not make a close approach (Hill pers. comm.). This may have increased
capture rate at traps without the acoustic lure due to heightened activity throughout the
woodland patch. The trapping of bats is important to confirm species identity, obtain
detailed information of populations/individuals (e.g. sex ratios and body condition), and
more accurate abundance estimates. We have demonstrated that the use of an acoustic
lure can improve surveying efficiency by maximising bat capture rates which will reduce the
money, time, and effort required whilst trapping. However, further research on whether
some species avoid certain call types and how this may vary between the sexes and
throughout the season would be useful in understanding any disruptive effect to bat
populations the acoustic lure could be having. We therefore support the suggestions of Hill
and Greenaway (2005) that call playback times should be brief and avoid frequent repetition
within the same location.

Effect of broadcasting different types of synthesised bat calls on capture rate

Although the acoustic lure increased total trapping success, there were significant
differences in the effectiveness of each type of synthesised bat call broadcast. All species
responded strongly to at least some heterospecific calls. This finding supports the work of
Schöner, Schöner and Kerth (2010) who found that $P. \text{auritus}$ showed responsiveness to
$Myotis$ calls, but contrasts with Ruczyński et al. (2009) who found little response of $P. \text{auritus}$ to any broadcast calls. The lack of responsiveness to broadcast $M. \text{nattereri}$ calls by
both $Pipistrellus$ species and $P. \text{auritus}$ demonstrated that bats perceived call types
differently rather than exhibiting a generic response to the acoustic lure regardless of call
type. If a specific bat species is the focus of trapping then knowledge of which playback calls
attract a particular species will be valuable in maximising its capture rate while minimising by-catch of alternate species. For example, a study with the aim of trapping only *P. pygmaeus* or *P. pipistrellus* should consider broadcasting *Pipistrellus* sp. calls due to its relative ineffectiveness in attracting other species, thereby minimising secondary disturbance. Likewise, the same study should consider avoiding the broadcasting of *N. leisleri* social calls due to its effectiveness at increasing capture rate across species. The development of new calls and a call library for the acoustic lure will further increase capture rates as knowledge of which calls are most effective increases.

**Effect of sex, age, and seasonality on trapping success of *P. pygmaeus* with an acoustic lure**

Determining the sex ratio and age structure of population is important, both for ecological studies and conservation purposes; for example, the presence of a lactating female in early summer can indicate that a maternity roost is close (Henry et al. 2002). This study found that the acoustic lure increased *P. pygmaeus* trapping success for both sexes and for adults and juveniles alike, supporting its use in estimating overall population sizes for this species. Bats of both sexes and all ages are known to respond to calls of conspecifics for a variety of reasons; these include contact calls between mothers and pups (Pfalzer and Kusch 2003), mating activity (Russ et al. 2003), and response to distress calls (Russ et al. 2004). The increase in trapping efficiency of the acoustic lure as the summer progresses for male *P. pygmaeus* may reflect a heightened responsiveness to surrounding bat calls as the peak breeding season (i.e. autumn) approaches. *Pipistrellus* social calls increase from July onwards as a consequence of mating activity (Russ et al. 2003). The increase in male capture rate may be a result of increased aggression to a perceived competitor; Sachteleben and Helversen von (2006) found that *P. pipistrellus* chase intruders out of their territory during
courtship displays which may suggest that *P. pygmaeus* are behaving similarly whilst reacting to the acoustic lure. A reduced responsiveness to the acoustic lure earlier in the summer may result in undersampling of male *P. pygmaeus* from a habitat or skewed sex ratio estimates if surveying is not conducted regularly throughout the field season.

**Conclusions**

By optimising surveying procedures it is possible to provide more informative insights into an areas’ biodiversity, minimise disturbance to wildlife, and to make surveying more cost and time effective. We have shown that acoustic surveys are a suitable surrogate for relative abundance for conspicuous species. We have shown, for certain species, that acoustic surveys are a suitable surrogate for relative abundance. However in woodlands the widespread presence of quiet species means they may be better suited to a complementary approach. Increasing capture rate by the use of an acoustic lure will minimise relative surveying effort and increase the biological and ecological understanding that can be made into an area’s bat population. We have demonstrated that species respond differently to the broadcasting of different call types; this will allow the future use of targeted calls to minimise disturbance to non-target species. Obtaining informative data on bat populations within woodland is known to be difficult; this study suggests a number of techniques that can improve surveying efficiency and consequently the awareness and knowledge of bat populations and how to best conserve them.

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References


Schöner, C.R., Schöner, M.G. & Kerth, G. (2010). Similar is not the same: Social calls of conspecifics are more effective in attracting wild bats to day roosts than those of other bat species. Behavioral Ecology Sociobiology 64, 2053-2063.


**Table 1. Species presence confirmed by multiple surveying methods**

Summary of confirmed species presence determined by trapping, acoustic surveys or combined methods at 68 woodlands in central Scotland. The percentage increase of the combined approach is calculated from the addition of sites where a species was detected by trapping but not by acoustic monitoring to sites where a species was only detected by acoustic monitoring.

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<thead>
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<th>Species</th>
<th>% of sites (number of sites) at which species presence confirmed</th>
<th>% increase of combined approach</th>
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<td>Acoustic</td>
<td>Combined</td>
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<th>% of sites (number of sites) at which species presence confirmed</th>
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25
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<th></th>
<th>Lure</th>
<th>No lure</th>
<th>Total</th>
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<td>82.4</td>
<td>91.2</td>
<td>94.2</td>
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<td>22.1</td>
<td>77.9</td>
<td>79.4</td>
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<td>16.2</td>
<td>27.9</td>
<td>41.2</td>
<td>44.1</td>
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<td>of which:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>M. nattereri</em></td>
<td>19.1</td>
<td>14.7</td>
<td>25</td>
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<tr>
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<td>2.9</td>
<td>4.4</td>
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<tr>
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<td>8.8</td>
<td>7.4</td>
<td>13.2</td>
<td>13.2</td>
<td>23.5</td>
</tr>
</tbody>
</table>

**Table 2.** Associations between bat capture rates and bat activity and date

Summary of results for linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis* sp. to assess whether an association exists between bat capture rate (response variable) and bat activity and if this changes with date. Significant values are highlighted in bold.
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<tr>
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<th>Model</th>
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<td>-</td>
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<td>-</td>
<td>0.026</td>
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<td><em>Myotis sp.</em></td>
<td>-0.102</td>
<td>0.477</td>
<td>-</td>
<td>-0.187</td>
<td>0.122</td>
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<td>-0.016</td>
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Model: 7.19% 1.06%
Fig. 1 Linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis* sp. to assess whether an association exists between bat capture rate and bat activity and if it changes through the season. The shaded area represents 95% confidence intervals for each model. Note the difference in axis scales between species.
Fig. 2 Bat captures per hour for four species, with and without the lure. The upper and lower hinges correspond to the first and third quartiles, while the upper and lower whiskers extend to the value that is within 1.5 times of the interquartile range of the hinge (Wickham 2012). Outliers are excluded from this graph. Significance codes: p ≤ 0.001***, p ≤ 0.01**, p ≤ 0.05*, p ≤ 0.1.
Fig. 3 The effectiveness of different call sequence types broadcast by the acoustic lure in capturing bats. Bats caught without the acoustic lure were not included within this analysis. The dashed line signifies the expected proportion of bats caught for each call type.
Fig. 4 Relationship between survey date and the difference in capture rate between *P. pygmaeus* bats caught with and without the acoustic lure for both sexes. The shaded area represents 95% confidence intervals for either sex. No trapping was conducted in late June to avoid capturing heavily pregnant females.