

1 **Testing the effectiveness of surveying techniques in determining bat community**
2 **composition within woodland** **Abridged title:** Methods to determine bat community
3 composition

4 **Paul R. Lintott^{AC}, Elisa Fuentes-Montemayor^A, Dave Goulson^B, Kirsty J. Park^A**

5 ^A Biological and Environmental Sciences, School of Natural Sciences, University of Stirling,
6 Scotland, FK9 4LA

7 ^B School of Life Sciences, University of Sussex, UK, BN1 9RH

8 ^C Corresponding author. Email: p.r.lintott@stir.ac.uk

9 **Abstract**

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

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

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

22 **Key results:** There was a significant positive relationship between bat activity recorded on
23 ultrasonic detectors and the number of individuals captured for *Pipistrellus pygmaeus* and *P.*
24 *pipistrellus*. Acoustic monitoring was more effective than trapping at determining species
25 presence, however to ensure rarer or quiet species are recorded a complementary
26 approach is required. Broadcasting four different types of echolocation call resulted in a 2 to
27 12 fold increase in trapping success across four species of insectivorous bat found in the

28 study region. Trapping success was dependent on the type of echolocation call that was
29 broadcast. There was no effect of sex or age on trapping success; however, whilst lure
30 effectiveness remained unchanged for female *P. pygmaeus*, there was a marked increase in
31 the number of males captured using the lure throughout the summer (May to September).

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

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

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

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54 **Introduction**

55 Obtaining accurate quantitative information on the species richness of an area is difficult,
56 yet it is essential to identify highly biodiverse areas which should be prioritised for
57 conservation (Brooks *et al.* 2006). Species can remain undetected despite extensive
58 surveying while presence records can be spatially biased towards localities that are easier to
59 survey or are more frequented by recorders (Rondinini *et al.* 2006). Estimates of species'
60 frequency of occurrence or relative abundance are also often used as indices of species
61 persistence to gain a better understanding of how species use habitats (Araújo and Williams
62 2000). Abundance has been used to form area-based priority-setting criteria for a range of
63 taxa (Gauthier *et al.* 2010). However assessing abundance for rare or elusive species
64 involves considerably more uncertainty and failure to detect species within an area may
65 influence future planning decisions and leave sites vulnerable to habitat loss. Many species
66 of European bat have undergone population declines in the past few decades due to habitat
67 loss and degradation, a consequence of pressure on resources from increasing human
68 populations (Mickleburgh *et al.* 2002). Bats are becoming of increasing importance as
69 bioindicators, therefore gaining accurate estimates of bat population sizes is critical to
70 quantify the extent of these declines (Jones *et al.* 2009). The size of bat populations can be
71 estimated by counting individuals emerging from summer roosts (Jones *et al.* 1996) or in
72 hibernacula (O'Shea *et al.* 2003), however roosts are often difficult to find and inaccessible.
73 Acoustic surveys using bat detectors are widely used in studies to determine species
74 presence and quantify activity of foraging bats (e.g. Roche *et al.* 2011; Fuentes-Montemayor

75 *et al.* 2012). However, call intensity varies between species; gleaning species such as
76 *Plecotus* spp. emit calls of short duration, high frequency, and low intensity which may not
77 be detected by acoustic surveys (Waters and Jones 1995). In cluttered habitats, such as
78 woodland, bats emit quieter echolocation calls, which can reduce detection rate and make
79 species identification from ultrasonic recordings more difficult (Russ 1999; Schnitzler and
80 Kalko 2001). Therefore, it is often necessary to confirm species presence within an area by
81 capturing and examining individuals in the hand.

82 Mist netting and harp trapping are two of the most common methods used to capture bats
83 (O'Farrell and Gannon 1999). However, as with acoustic surveys, inherent biases exist within
84 these sampling techniques including interspecies differences in capture rates (Berry *et al.*
85 2004), avoidance-learning behaviour in bats (Larsen *et al.* 2007), and ambient light levels
86 altering net detectability (Lang *et al.* 2004). Habitat characteristics can also determine
87 capture rates; trapping is most effective in locations with dense vegetation containing
88 discrete flyways (Duffy *et al.* 2000; Hourigan *et al.* 2008). However, some species, such as
89 *Myotis bechsteinii*, rarely use tracks or rides which would therefore decrease their capture
90 rate when surveying within woodland habitat (Hill and Greenaway 2005). Additionally,
91 trapping requires specialist skills, and can cause stress to the animals (Flaquer *et al.* 2007).

92 A complementary approach, using a combination of acoustic surveys and trapping
93 techniques, is often found to maximise detection efficiency (Duffy *et al.* 2000; MacSwiney *et*
94 *al.* 2008; Meyer *et al.* 2011), yet is not always practical due to limitations in expertise,
95 expense, and time requirements (Hourigan *et al.* 2008). Therefore a number of previous
96 studies have used measurements of bat activity assessed by acoustic monitoring as a
97 surrogate for relative abundance (e.g. Kalko *et al.* 2008; Razgour *et al.* 2011; Berthinussen

98 and Altringham 2012), however to our knowledge this relationship has not been explicitly
99 tested.

100 Broadcasting natural or synthetic auditory stimuli has been used to increase detection rates
101 by provoking a response that makes individuals more easily detectable. Such “playback”
102 calls have been used to estimate population sizes in a range of amphibian, avian, and
103 mammalian species including *Bufo marinus* (Schwarzkopf and Alford 2007), *Loxia scotica*
104 (Summers and Buckland 2011), and *Panthera leo* (Brink *et al.* 2012). Behavioural studies
105 have demonstrated that the broadcasting of bat feeding buzzes and social calls can attract
106 both conspecific and heterospecific bats (Russ *et al.* 1998; Wilkinson and Boughman 1998);
107 this led to the development of an acoustic lure, the Sussex AutoBat (Hill and Greenaway
108 2005). Field testing found that the capture rate of different bat species, including the rare
109 *M. bechsteinii*, increased with the use of an acoustic lure (Hill and Greenaway 2005; Goiti *et*
110 *al.* 2007; Hill and Greenaway 2008), but the extent to which this lure enhances capture rates
111 in comparison to traditional trapping techniques has not, to our knowledge, been
112 systematically tested.

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

- 117 1. Is bat activity, as measured by acoustic surveys, a good surrogate for relative bat
118 abundance?
- 119 2. Which surveying method (acoustic surveys or trapping) is most effective at
120 determining species presence within temperate woodland?

- 121 3. To what extent does an acoustic lure enhance capture rate in comparison to
122 traditional trapping techniques?
- 123 4. Does the type of synthesised bat call broadcast determine capture rate?
- 124 5. What is the effect of sex, age, and seasonality on trapping success with an acoustic
125 lure?

126 **Materials and methods**

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

140 An estimate of relative abundance was determined by placing an Austbat harp trap (2.4 x
141 1.8 m) and three Ecotone mist nets (2.4 x 6 m each) within each woodland. Traps were
142 placed ≥ 20 m from the woodland edge, ≥ 40 m from each other and positioned to avoid
143 paths and obvious flyways (i.e. rides and trails). An acoustic lure (The Autobat, Sussex

144 University) was positioned alongside a trap and moved between traps every 30 minutes for
145 the duration of surveying (Hill and Greenway 2005). Preliminary testing using a frequency
146 division bat detector indicated that the sound emitted by the acoustic lure was detectable
147 from a maximum of 20 m away, although it is likely that bats can hear them from a greater
148 distance (i.e. Murphy 2012). Four different synthesised bat call types were played
149 (*Pipistrellus* sp. mix, *Myotis* sp. mix, *Nyctalus leisleri*, and *M. nattereri*), which are known to
150 attract a variety of bat species (Greenaway pers. comm.). Call sequences were switched
151 every 15 minutes and played in the same sequence each night. Traps were checked every 15
152 minutes to extract any captured bats, which were then identified to species, aged, sexed,
153 measured, weighed and marked temporarily by fur clipping. All procedures were
154 preapproved by the University of Stirling ethical review committee and all bats were caught
155 under Scottish Natural Heritage Scientific License.

156 Bat activity was quantified using a frequency division bat detector (Anabat SD1, Titley
157 Electronics) fixed on a 1 m high pole with the microphone pointing upwards. The detector
158 was positioned adjacent to the centre of the trap (< 1 m away) and rotated between traps
159 every 30 minutes. The sequence of rotation ensured the detector did not record at the same
160 net as the acoustic lure was positioned. All bat recordings were analysed using Anabook W
161 (Corben 2006). One bat pass was defined as a continuous sequence of at least two
162 echolocation calls from a passing bat (Walsh & Harris 1996). All nine species of four bat
163 genera present within the study area (*Myotis*, *Nyctalus*, *Pipistrellus*, and *Plecotus*) can be
164 identified from detector recordings based upon the search-phase of their echolocation call
165 (Russ 1999). However, it can often be difficult to distinguish between *Myotis* species due to
166 similarities in call structure, particularly within cluttered environments (Schnitzler and Kalko

167 2001). As a consequence, recordings of *Myotis* species known to be present in the area (*M.*
168 *daubentonii*, *M. mystacinus*, and *M. nattereri*) were grouped together as *Myotis* sp. The
169 three *Pipistrellus* species in this area (*P. pipistrellus*, *P. pygmaeus* and *P. nathusii*) can be
170 determined by the characteristic frequency (F_c = the frequency at the right hand end of the
171 flattest portion of a call; Corben 2006) of their search-phase echolocation calls. Bat passes
172 with a F_c of between 49 and 51 kHz were classed as unknown *Pipistrellus* sp..

173 Statistical analyses were conducted using the statistics package R version 2.14 (R Core Team
174 2012) run within the R Studio interface (R Studio 2012) and using the package ggplot2
175 (Wickham 2009). Total captures per site was converted to captures per hour per site
176 (with/without the acoustic lure) as the lure was only operating at one of the four traps at a
177 time within each site. Total bat passes per site was converted to passes per hour. We
178 performed a series of linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis*
179 sp. to determine whether an association exists between bat capture rate and bat activity
180 and if it changes through the season. Bat captures per hour per site was used as the
181 response variable for each species / genus. Bat activity, date and the interaction between
182 them were included as predictor variables in each of the models. Each model was fitted with
183 a Gaussian distribution and if required the capture and activity rates were logged to achieve
184 normality. Non-significant interactions or variables were removed from the model using a
185 step-wise method whereby explanatory variables were dropped or retrained using $P \leq 0.05$
186 as a threshold. Model validation was conducted by the examination of residuals (Zuur *et al.*
187 2009). To determine how the effectiveness of each surveying strategy varies between
188 species we compared the number of woodlands in which species presence was confirmed
189 by either trapping (with and without the lure), acoustic surveys, or both methods combined.

190 A Mann Whitney U-test was used to determine if the number of species detected per site
191 differed between surveying method. A two-sided Wilcoxon paired test was used to assess
192 trapping success with and without the acoustic lure for each species / genus. The relative
193 effectiveness of the four different synthesised bat call types broadcast by the acoustic lure
194 was tested using a chi-square test. To determine whether trapping success with and without
195 the acoustic lure varied between sex or age (adult / juvenile), two-sided Wilcoxon paired
196 tests were conducted on *P. pygmaeus* only as there were insufficient numbers of other
197 species captured. We also tested whether the effect of the lure on male and female *P.*
198 *pygmaeus* changed with date throughout the active season using linear regressions for
199 males and females separately. Regression models were validated by visual examination of
200 residuals (Crawley 2007).

201 **Results**

202 *Bat activity and abundance*

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

213 (Insert Table 1)

214 *Correspondence between acoustic surveys and capture rates*

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

220 (Insert Table 2 and Figure 1)

221 *Effectiveness of surveying methods at determining species presence*

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

231 *Effect of an acoustic lure on capture rate*

232 The acoustic lure significantly increased capture rates for all species. *P. pygmaeus* showed
233 the strongest response ($n= 56$, $v=1593$, $p = 0.001$) with a 12-fold increase in individuals

234 caught using the acoustic lure. Likewise, 7.5x more *P. pipistrellus* were caught when the lure
235 was adjacent to a trap (n= 15, v= 117, p =0.001). The acoustic lure increased the capture
236 rate of both *M. nattereri* (n=17, v=127, p=0.017) and *P. auritus* (n=9, v=39, p=0.055) by
237 2.25x and 3.5x respectively (Fig 2).

238 (Insert Figure 2)

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

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

250 (Insert Figure 3)

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

252 The acoustic lure significantly increased the capture rate of both male (n= 51, v=1316, p =
253 0.001), and female (n= 39, v=702, p = 0.001) *P. pygmaeus*. Broadcasting synthesised bat calls
254 also significantly increased the capture rate of both juvenile (n= 23, v=273, p = 0.001), and
255 adult (n= 54, v=1482, p = 0.002) *P. pygmaeus*. The effectiveness of the acoustic lure for

256 female *P. pygmaeus* did not vary across the active season ($F_{1,55} = 1.04$, $p = 0.321$), but males
257 responded more strongly to the lure later in the summer than in the spring ($F_{1,48} = 20.3$, $p =$
258 $= 0.001$, $r^2 = 0.3$; Fig 4).

259 (Insert Figure 4)

260 **Discussion**

261 *Bat activity and abundance*

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

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

275 Acoustic surveys are widely used in field studies to act as an index of relative abundance
276 however the relationship between these two indices is rarely tested (e.g. Kalko *et al.* 2008).
277 Trapping can be a costly and time consuming process requiring expertise whilst acoustic

278 surveys are non-intrusive and comparatively simple. Here, we showed that, in the case of *P.*
279 *pygmaeus* and *P. pipistrellus*, activity levels vary positively with relative abundance and
280 could be used a surrogate for abundance to increase surveying efficiency. This provides
281 additional support that surveys monitoring population change over time (e.g. Bat
282 Conservation Trust's Field Survey, part of a suite of surveys in the National Bat Monitoring
283 Programme (Bat Conservation Trust 2013)) are reflecting relative changes in bat populations
284 despite only using acoustic surveys. A significant relationship was found between *P.*
285 *pygmaeus* capture rate and date which may reflect a heightened response to the acoustic
286 lure with date as discussed below. There was no significant relationship between *Myotis* sp.
287 activity and capture rate. This is unsurprising given that each species within this group is
288 likely to have varying levels of detection by acoustic surveys (e.g. flight height) and capture
289 rates (e.g. differing responses to an acoustic lure). Combining the data into a larger species
290 group will therefore mask any species specific relationship between activity and capture
291 rate from being observed.

292 *Effectiveness of surveying methods at determining species presence*

293 Although using multiple surveying methods can maximise species detection efficiency
294 (MacSwiney *et al.* 2008; Meyer *et al.* 2011), it is often impractical. This study demonstrates
295 that a complementary approach can be unnecessary if the aim of surveying is to determine
296 the presence of conspicuous species within a habitat. For instance, we found only a
297 marginal benefit of undertaking both acoustic surveys and trapping for *P. pipistrellus* and *P.*
298 *pygmaeus*. Given that bat detectors are cost effective, can be automated to run for long
299 time periods, and are non-intrusive (Hourigan *et al.* 2008), acoustic surveys alone are a
300 satisfactory method for surveys which focus on a specific conspicuous species. In

301 comparison, accurately determining bat community composition or the presence of quiet
302 species such as *P. auritus* might require a complementary approach. This supports the work
303 by Flaquer *et al.* (2007) who found that rarer species are often only detected by one
304 method, which suggests they could be easily overlooked if only one sampling technique is
305 used. Additionally, trapping can provide confirmation to species level for every individual
306 captured, in contrast to acoustic surveys which in some cases can be problematic in
307 achieving this level of accuracy due to call similarities between species (Walters *et al.* 2012).
308 In addition, the effectiveness of each surveying method may differ depending upon the
309 habitat type that they are used in (e.g. between open and closed habitat).

310 *Effect of an acoustic lure on capture rate*

311 The acoustic lure greatly increased bat capture rate, with between a 2 and 12 fold increase
312 in trapping success across species. Bats are known to respond to conspecific and
313 heterospecific calls (Fenton 2003, Dechmann *et al.* 2009; Knörnschild *et al.* 2012) and the
314 acoustic lure appeared to invoke a similar response to the synthesised calls that were
315 played. Although we demonstrated the effectiveness of the lure in increasing bat capture
316 rate, the ecological mechanism by which it works is currently unknown. A response may
317 have occurred due to bats eavesdropping on surrounding calls to locate food sources
318 (Gillam 2007), or acting aggressively to a perceived competitor (Hill and Greenway 2005).
319 Additionally it is plausible that the lure may be impairing the bats' ability to echolocate
320 thereby masking the position or presence of the trap. Mist nets and harp traps are
321 conspicuous acoustic targets to bats (Berry *et al.* 2004); detection rates may therefore be
322 reduced by an increased external sensory input. Bats exhibit high rates of trap avoidance
323 (Larsen *et al.* 2007), which the use of an acoustic lure appears to reduce. It is likely that we

324 have underestimated the effectiveness of the acoustic lure given that some bats respond to
325 the lure but do not make a close approach (Hill pers. comm.). This may have increased
326 capture rate at traps without the acoustic lure due to heightened activity throughout the
327 woodland patch. The trapping of bats is important to confirm species identity, obtain
328 detailed information of populations/individuals (e.g. sex ratios and body condition), and
329 more accurate abundance estimates. We have demonstrated that the use of an acoustic
330 lure can improve surveying efficiency by maximising bat capture rates which will reduce the
331 money, time, and effort required whilst trapping. However, further research on whether
332 some species avoid certain call types and how this may vary between the sexes and
333 throughout the season would be useful in understanding any disruptive effect to bat
334 populations the acoustic lure could be having. We therefore support the suggestions of Hill
335 and Greenaway (2005) that call playback times should be brief and avoid frequent repetition
336 within the same location.

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

338 Although the acoustic lure increased total trapping success, there were significant
339 differences in the effectiveness of each type of synthesised bat call broadcast. All species
340 responded strongly to at least some heterospecific calls. This finding supports the work of
341 Schöner, Schöner and Kerth (2010) who found that *P. auritus* showed responsiveness to
342 *Myotis* calls, but contrasts with Ruczyński *et al.* (2009) who found little response of *P.*
343 *auritus* to any broadcast calls. The lack of responsiveness to broadcast *M. nattereri* calls by
344 both *Pipistrellus* species and *P. auritus* demonstrated that bats perceived call types
345 differently rather than exhibiting a generic response to the acoustic lure regardless of call
346 type. If a specific bat species is the focus of trapping then knowledge of which playback calls

347 attract a particular species will be valuable in maximising its capture rate while minimising
348 by-catch of alternate species. For example, a study with the aim of trapping only *P.*
349 *pygmaeus* or *P. pipistrellus* should consider broadcasting *Pipistrellus* sp. calls due to its
350 relative ineffectiveness in attracting other species, thereby minimising secondary
351 disturbance. Likewise, the same study should consider avoiding the broadcasting of *N.*
352 *leisleri* social calls due to its effectiveness at increasing capture rate across species. The
353 development of new calls and a call library for the acoustic lure will further increase capture
354 rates as knowledge of which calls are most effective increases.

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

356 Determining the sex ratio and age structure of population is important, both for ecological
357 studies and conservation purposes; for example, the presence of a lactating female in early
358 summer can indicate that a maternity roost is close (Henry *et al.* 2002). This study found that
359 the acoustic lure increased *P. pygmaeus* trapping success for both sexes and for adults and
360 juveniles alike, supporting its use in estimating overall population sizes for this species. Bats
361 of both sexes and all ages are known to respond to calls of conspecifics for a variety of
362 reasons; these include contact calls between mothers and pups (Pfalzer and Kusch 2003),
363 mating activity (Russ *et al.* 2003), and response to distress calls (Russ *et al.* 2004). The
364 increase in trapping efficiency of the acoustic lure as the summer progresses for male *P.*
365 *pygmaeus* may reflect a heightened responsiveness to surrounding bat calls as the peak
366 breeding season (i.e. autumn) approaches. *Pipistrellus* social calls increase from July
367 onwards as a consequence of mating activity (Russ *et al.* 2003). The increase in male capture
368 rate may be a result of increased aggression to a perceived competitor; Sachteleben and
369 Helversen von (2006) found that *P. pipistrellus* chase intruders out of their territory during

370 courtship displays which may suggest that *P. pygmaeus* are behaving similarly whilst
371 reacting to the acoustic lure. A reduced responsiveness to the acoustic lure earlier in the
372 summer may result in undersampling of male *P. pygmaeus* from a habitat or skewed sex
373 ratio estimates if surveying is not conducted regularly throughout the field season.

374 **Conclusions**

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

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400 **References**

401 Araújo, M.B. & Williams, P.H. (2000). Selecting areas for species persistence using
402 occurrence data. *Biological Conservation* **96**, 331-345.

403 Bat Conservation Trust. (2013). The National Bat Monitoring Programme. Annual Report
404 2012. Bat Conservation Trust, London. (www.bats.org.uk)

405 Berry, N., O'Connor, W., Holderied, M.W. & Jones, G. (2004). Detection and avoidance of
406 harp traps by echolocating bats. *Acta Chiropterologica* **6**, 335-346.

407 Berthinussen, A. & Altringham, J. (2012). The effect of a major road on bat activity and
408 diversity. *Journal of Applied Ecology* **49**, 82–89.

409 Brink, H., Smith, R. J. & Skinner, K. (2012). Methods for lion monitoring: a comparison from
410 the Selous Game Reserve, Tanzania. *African Journal of Ecology* **51**, 366-375.

411 Brooks, T.M., Mittermeier, R.A., Fonseca da, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux,
412 J.F., Mittermeier, C.G., Pilgram, J.D., & Rodrigues, A.S.L. (2006). Global biodiversity
413 conservation priorities. *Science* **313**, 58-61

414 Corben, C. (2006). AnlookW for bat call analysis using ZCA version 3.3f,
415 <http://www.hoarybat.com> (accessed November 2012).

416 Crawley, M.J., (2007). The R Book. John Wiley & Sons, West Sussex.

417 Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C. & Wikelski, M. (2009).
418 Experimental evidence for group hunting via eavesdropping in echolocating bats.
419 *Proceedings of the Royal Society: Biological Sciences* **276**, 2721-2728.

420 Duffy, A.M., Lumsden, L.F., Caddle, C.R., Chick, R.R, & Newell, G.R. (2000). The efficacy of
421 Anabat ultrasonic detectors and harp traps for surveying microchiropterans in south-eastern
422 Australia. *Acta Chiropterologica* **2**, 127-144.

423 EDINA Digimap Ordnance Survey Service. OS MasterMap Topography Layer.
424 <http://edina.ac.uk/digimap> (accessed November 2012).

425 Fenton, M. B. (2003). Eavesdropping on the echolocation and social calls of bats. *Mammal*
426 *Review* **33**, 193-204.

427 Flaquer, C., Torre, I. & Arrizabalaga, A. (2007). Comparison of sampling methods for
428 inventory of bat communities. *Journal of Mammalogy* **88**, 526-533.

429 Fuentes-Montemayor E, Goulson D, Cavin L, Wallace J.M. & Park K.J. (2012). Factors
430 influencing moth assemblages in woodland fragments on farmland: implications for
431 woodland creation and management schemes. *Biological Conservation* **153**, 265-275.

432 Gauthier, P., Debussche, M. & Thompson, J.D. (2010). Regional priority setting for rare
433 species based on a method combining three criteria. *Biological Conservation* **143**, 1501-
434 1509.

435 Gillam, E.H. (2007). Eavesdropping by bats on the feeding buzzes of conspecifics. *Canadian*
436 *Journal of Zoology* **85**, 795-801.

437 Goiti, U., Aihartza, J., Garin, I. & Salsamendi, E. (2007). Surveying for the rare Bechstein's bat
438 (*Myotis bechsteinii*) in northern Iberian peninsula by means of an acoustic lure. *Hystrix* **18**,
439 215-223.

440 Gu, W & Swihart, R.K. (2004). Absent or undetected? Effects of non-detection of species
441 occurrence on wildlife-habitat models. *Biological Conservation* **116**, 195-203.

442 Henry, M., Thomas, D.W., Vaudry, R. & Carrier, M. (2002). Foraging distances and home
443 range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy*
444 **83**, 767-774.

445 Hill, D. A. & Greenaway, F. (2005). Effectiveness of an acoustic lure for surveying bats in
446 British woodlands. *Mammal Review* **35**, 116–122.

447 Hill, D. A. & Greenaway, F. (2008). Conservation of bats in British woodlands. *British Wildlife*
448 **19**, 161-169.

449 Hourigan, C.L., Catterall, C.P., Jones, D. & Rhodes, M. (2008). Comparisons of harp trap and
450 bat detector efficiency for surveying bats in an urban landscape. *Wildlife Research* **35**, 768-
451 774.

452 Jones, K. E., Altringham, J. D. & Deaton, R. (1996). Distribution and population densities of
453 seven species of bat in northern England. *Journal of Zoology* **240**, 788–798.

454 Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R. & Racey, P.A. (2009). Carpe noctem: the
455 importance of bats as bioindicators. *Endangered Species Research* **8**, 93-115.

456 Kalko, E.K.V., Villegas, S.E., Schmidt, M., Wegmann, M. & Meyer, C.F.J. (2008). Flying high –
457 assessing the use of the aerosphere by bats. *Integrative and Comparative Biology* **48**, 60-73.

458 Knörnschild, M., Jung, K., Nagy, M., Metz, M. & Kalko, E. (2012). Bat echolocation calls
459 facilitate social communication. *Proceedings of the Royal Society: Biological Sciences* **279**,
460 4827-4835.

461 Lang, A.B., Weise, C.D., Kalko, E.K.V. & Roemer, H. (2004). The bias of bat netting. *Bat*
462 *Research News* **45**, 235-236.

463 Larsen, R.J., Boegler, K.A., Genoways, H.H., Masefield, W.P., Kirsch, R.A. & Pedersen, S.C.
464 (2007). Mist netting bias, species accumulation curves, and the rediscovery of two bats on
465 Montserrat (Lesser Antilles). *Acta Chiropterologica* **9**, 423-435.

466 MacSwiney G., M.C., Clarke, F.M., & Racey, P.A. (2008). What you see is not what you get:
467 the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat
468 assemblages. *Journal of Applied Ecology* **45**, 1364-1371.

469 Magurran, A.E. & Henderson, P.A.(2003). Explaining the excess of rare species in natural
470 species abundance distributions. *Nature* **422**, 714-716.

471 McCabe, D. J. (2012). Sampling Biological Communities. *Nature Education Knowledge* **3**, 63

472 Meyer, C.F.J., Aguiar, L.M.S., Aguirre, L.F., Baumgarten, J., Clarke, F.M., Cosson, J.- F.,
473 Villegas, S.E., Fahr, J., Faria, D., Furey, N., Henry, M., Hodgkison, R., Jenkins, R.K.B., Jung,
474 K.G., Kingston, T., Kunz, T.H., MacSwiney Gonzalez, M.C., Moya, I., Patterson, B.D., Pons, J.-
475 M., Racey, P.A., Rex, K., Sampaio, E.M., Solari, S., Stoner, K.E., Voigt, C.C., von Staden, D.,
476 Weise, C.D., & Kalko, E.K.V. (2011). Accounting for detectability improves estimates of
477 species richness in tropical bat surveys. *Journal of Applied Ecology* **48**, 777-787.

478 Mickleburgh, S.P., Hutson, A.M. & Racey, P.A. (2002). A review of the global conservation
479 status of bats. *Oryx* **36**, 18-34.

480 Murphy, S.E. (2012). Function of social calls in Brown Long-eared bats *Plecotus auritus*.
481 Doctoral thesis, University of Sussex.

482 O'Farrell, M.J. & Gannon, W.L. (1999). A comparison of acoustic versus capture techniques
483 for the inventory of bats. *Journal of Mammalogy* **80**, 24-30.

484 O'Shea, T.J., Bogan, M.A. & Ellison, L.E. (2003). Monitoring trends in bat populations of the
485 United States and territories: status of the science and recommendations for the future.
486 *Wildlife Society Bulletin* **31**, 16-29.

487 Pfalzer, G. & Kusch, J. (2003). Structure and variability of bat social calls: implications for
488 specificity and individual recognition. *Journal of Zoology* **261**, 21-33.

489 R Core Team (2012). R: A language and environment for statistical computing. R Foundation
490 for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)
491 [project.org/](http://www.R-project.org/).

492 Razgour, O.N., Korine, C. & Saltz, D. (2011). Does interspecific competition drive patterns of
493 habitat use in desert bat communities? *Oecologia* **167**, 493 – 502.

494 Roche, N., Langton, S., Aughney, T., Russ, J. M., Marnell, F., Lynn, D., & Catto, C. (2011). A
495 car-based monitoring method reveals new information on bat populations and distributions
496 in Ireland. *Animal Conservation* **14**, 642-651.

497 Rondinini, C., Wilson, K. A., Boitani, L., Grantham, H. & Possingham, H. P. (2006). Tradeoffs
498 of different types of species occurrence data for use in systematic conservation planning.
499 *Ecology Letters* **9**, 1136–1145.

500 RStudio (2012). RStudio: Integrated development environment for R (Version 0.96.122)
501 [Computer software]. Boston, MA. Available from <http://www.rstudio.org/> (accessed May
502 2012).

503 Ruczyński, I., Kalko, E.K.V., Siemers, B.M. (2009). Calls in the Forest: A Comparative
504 Approach to How Bats Find Tree Cavities. *Ethology* **115**, 167-177.

505 Russ, J.M. (1999). The Bats of Britain & Ireland. Echolocation Calls, Sound Analysis, and
506 species Identification. (Alana Ecology: Powys).

507 Russ, J. M., Briffa, M. & Montgomery, W. I. (2003). Seasonal patterns in activity and habitat
508 use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a
509 driven transect. *Journal of Zoology* **259**, 289–299.

510 Russ, J.M., Jones, G., Mackie, I.J. & Racey, P.A. (2004). Interspecific responses to distress
511 calls in bats (Chiroptera: Vespertilionidae): a function for convergence in call design? *Animal*
512 *Behaviour* **67**, 1005-1014.

513 Russ, J.M., Racey, P.A. & Jones, G. (1998). Intraspecific responses to distress calls of the
514 pipistrelle bat, *Pipistrellus pipistrellus*. *Animal Behaviour* **55**, 705–713.

515 Sachteleben, J. & Helversen von, O. (2006). Songflight behaviour and mating system of the
516 pipistrelle bat (*Pipistrellus pipistrellus*) in an urban habitat. *Acta Chiropterologica* **8**, 391-
517 401.

518 Schnitzler, H.U. & Kalko, E.K.V. (2001). Echolocation by insect-eating bats. *BioScience* **51**,
519 557-569.

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

523 Schwarzkopf, L. & Alford, R.A. (2007). Acoustic attractants enhance trapping success for
524 cane toads. *Wildlife Research* **34**, 366-370.

525 Summers, R.W. & Buckland, S.T. (2011). A first survey of the global population size and
526 distribution of the Scottish Crossbill *Loxia scotica*. *Bird Conservation International* **21**, 186-
527 198.

528 Walsh, A.L. & S. Harris. (1996). Determinants of vespertilionid bat abundance in Britain:
529 geographic, land class and local habitat relationships (II). *Journal of Applied Ecology* **33**, 519-
530 529.

531 Walters, C. L., Freeman, R., Collen, A., Dietz, C., Brock Fenton, M., Jones, G., Obrist, M. K.,
532 Puechmaille, S. J., Sattler, T., Siemers, B. M., Parsons, S. & Jones, K. E. (2012). A continental-

533 scale tool for acoustic identification of European bats. *Journal of Applied Ecology* **49**, 1064–
 534 1074.

535 Waters, D.A. & Jones, G. (1995). Echolocation call structure and intensity in five species of
 536 insectivorous bats. *The Journal of Experimental Biology* **198**, 475-489.

537 Wickham. H. (2009). *ggplot2: elegant graphics for data analysis*. (Springer: New York.)

538 Wilkinson, G.S. & Boughman, J.W. (1998). Social calls coordinate foraging in greater spear-
 539 nosed bats. *Animal Behaviour* **55**, 337–350.

540 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed effects models
 541 and extensions in ecology with R*. (Springer Science+Business Media: New York.)

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

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

Species	% of sites (number of sites) at which species presence confirmed			% increase of combined approach
	Trapping	Acoustic	Combined	

	Lure	No lure	Total	survey	approach	
<i>P. pygmaeus</i>	80.9 (55)	38.2 (26)	82.4 (56)	91.2 (62)	94.2 (64)	3.2
<i>P. pipistrellus</i>	19.1 (13)	8.8 (6)	22.1 (15)	77.9 (53)	79.4 (54)	1.9
<i>Myotis sp.</i>	20.6 (14)	16.2 (11)	27.9 (19)	41.2 (28)	44.1 (30)	7.1
of which:						
<i>M. nattereri</i>	19.1 (13)	14.7 (10)	25 (17)			-
<i>M. daubentonii</i>	1.5 (1)	2.9 (2)	4.4 (3)			-
<i>M. mystacinus</i>	1.5 (1)	0 (0)	1.5 (1)			-
<i>P. auritus</i>	8.8 (6)	7.4 (5)	13.2 (9)	13.2 (9)	23.5 (16)	77.7

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

555 Summary of results for linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis*
556 *sp.* to assess whether an association exists between bat capture rate (response variable) and
557 bat activity and if this changes with date. Significant values are highlighted in bold.

Species	Predictor variable	95% CI			<i>p</i>	R ²
		Estimate	Lower	Upper		
<i>P. pygmaeus</i>	Activity	0.041	0.028	0.055	0.003	-
	Date	0.468	0.333	0.603	0.001	-
	Model	-	-	-	0.001	24.02%

<i>P.pipistrellus</i>	Activity	0.017	0.009	0.026	0.052	-
	Date	-0.023	-0.112	0.067	0.802	-
	Model	-	-	-	0.052	7.19%
<i>Myotis sp.</i>	Activity	-0.102	-0.187	-0.016	0.245	-
	Date	0.477	0.122	0.831	0.190	-
	Model	-	-	-	0.218	1.06%

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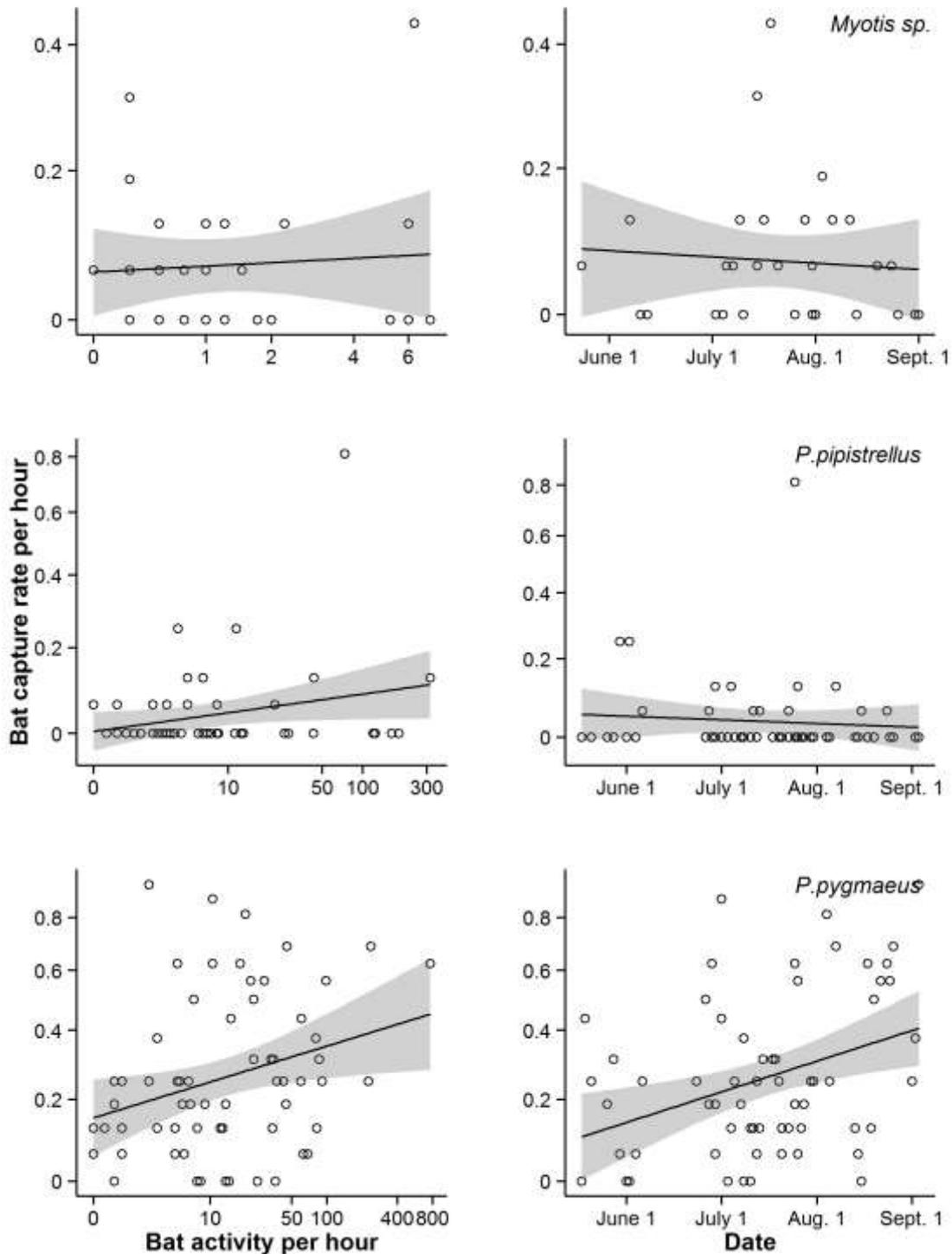
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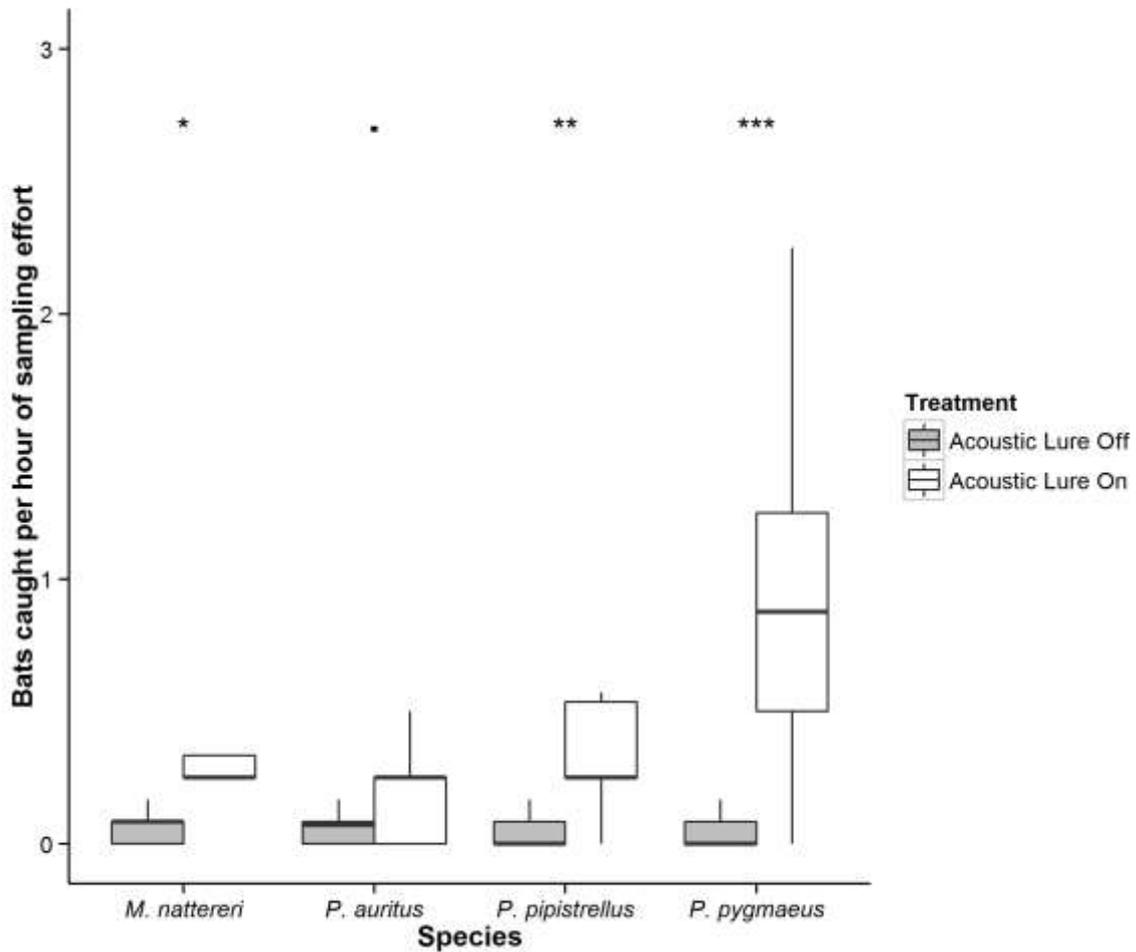


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565 **Fig. 1** Linear regression models for *P. pygmaeus*, *P. pipistrellus*, and *Myotis sp.* to assess whether an
 566 association exists between bat capture rate and bat activity and if it changes through the season.

567 The shaded area represents 95% confidence intervals for each model. Note the difference in axis

568 scales between species.



569

570 **Fig. 2** Bat captures per hour for four species, with and without the lure. The upper and lower hinges
 571 correspond to the first and third quartiles, while the upper and lower whiskers extend to the value
 572 that is within 1.5 times of the interquartile range of the hinge (Wickham 2012). Outliers are excluded
 573 from this graph. Significance codes: $p \leq 0.001$ ***, $p \leq 0.01$ ** , $p \leq 0.05$ *, $p \leq 0.1$.

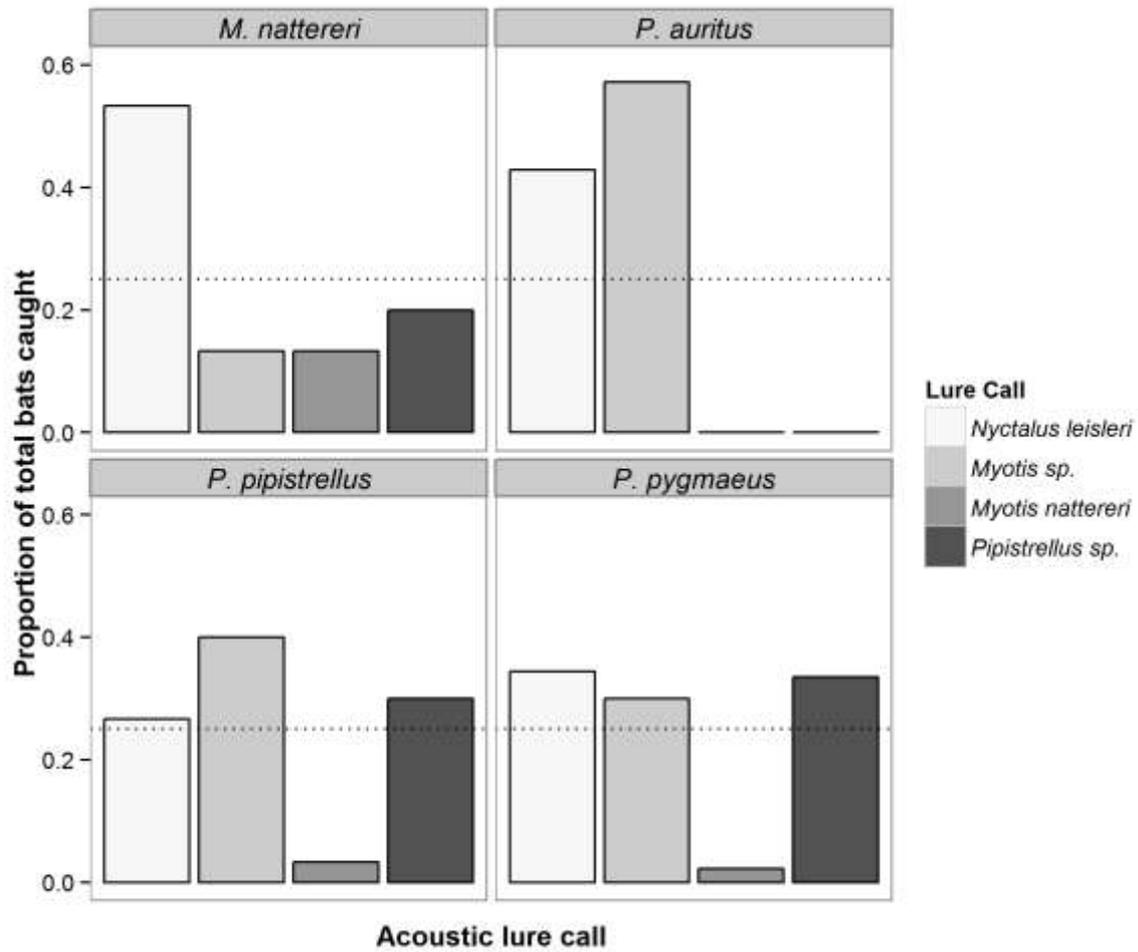
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580 **Fig. 3** The effectiveness of different call sequence types broadcast by the acoustic lure in capturing
 581 bats. Bats caught without the acoustic lure were not included within this analysis. The dashed line
 582 signifies the expected proportion of bats caught for each call type.

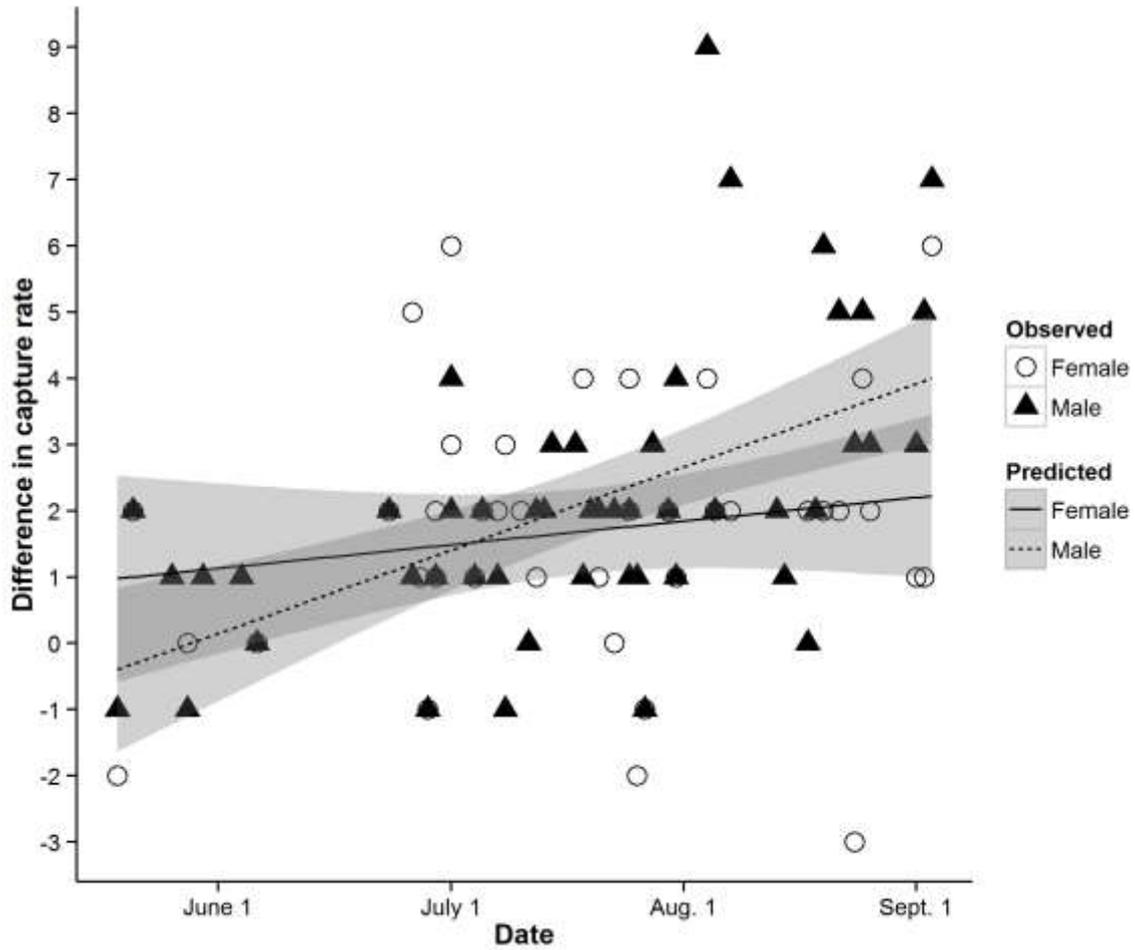
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589 **Fig. 4** Relationship between survey date and the difference in capture rate between *P. pygmaeus*
 590 bats caught with and without the acoustic lure for both sexes. The shaded area represents 95%
 591 confidence intervals for either sex. No trapping was conducted in late June to avoid capturing heavily
 592 pregnant females.

593