



## **Later is Better: Optimal Timing for Walked Activity Surveys for a European Bat Guild**

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## Later is better: optimal timing for walked activity surveys for a European bat guild

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Bat activity surveys (walked surveys combining transect and point counts) are extremely important for collecting data throughout Europe in conservation and planning contexts. To ensure optimal data, it is vital to ensure synchronicity between survey time and peak bat activity. However, although protocols for two-hour dusk activity surveys are well accepted, recommended start time in relation to sunset is a 'best guess' rather than based on empirical evidence. Accepted practice differs widely with recommended start times varying from 30 min pre-sunset (finishing 90 min post-sunset) to 30 min post-sunset (finishing 2.5 h after sunset). We provide the first empirical test of optimal start times for dusk activity surveys by comparing bat activity at the same sites on the same nights. Four sites were surveyed, viz. two high-quality woodland sites and two low-quality agricultural sites. At each site, surveyors walked the same route and stopped at the same pre-defined listening points for three repeat surveys per night: 1) starting 30 min pre-sunset; 2) starting at sunset; and 3) starting 30 min post-sunset. In total, 240 hours' of data were collected. Four species, all widespread and common throughout Europe, were recorded: common pipistrelle *Pipistrellus pipistrellus*, soprano pipistrelle *P. pygmaeus*, Natterer's *Myotis nattereri* and noctule *Nyctalus noctule*. Recorded bat activity was highest on sunset and post-sunset surveys both generally (overall bat activity) and for all specific species encountered. Findings were generally consistent for both low- and high-quality habitats. The same species were generally represented in both point and transect data but point data yielded higher estimates of overall activity in low-quality habitat and higher bat species richness in both high- and low-quality habitat relative to transect data. We recommend that: 1) two-hour dusk bat activity surveys start at/after sunset not before sunset and 2) both transect and point data are collected and analysed.

Bat surveys are used to inform conservation and development planning decisions. Within a conservation context, surveys are used to map species' distributions, monitor population change, and assess ecological value (Hutson et al. 2001, Walsh et al. 2004). Bat biodiversity is also an important bioindicator of habitat quality and ecosystem health (Racey and Entwistle 2005, Lacki et al. 2007) and indeed, bat population trends are increasingly being used Europe-wide as biodiversity indicators as per the 2010 EUROBATS resolution (review by European Environment Agency 2013). Within a planning context, surveys are used within an Environmental Impact Assessment to quantify baseline conditions, assess development impacts, and inform mitigation/compensation processes. Statutory Nature Conservation Organisations are then able to make informed decisions about whether licences to undertake activities detrimental to bat roosts (and sometimes feeding grounds and commuting pathways) should be granted (Bat Conservation Trust 2012). This ensures compliance with the EC Habitats Directive (92/43/EEC) and European Protected Species licensing framework, as well as the national legislation through which these are implemented.

In the temperate zone, bat surveys typically fall into main three groups: 1) identification and inspection of day roosts, maternity roosts, and hibernacula; and 2) passive acoustic surveys to identify commuting pathways and feeding grounds using automated ultrasonic detectors; and 3) surveys of bat activity in the wider countryside using handheld ultrasonic detectors (these usually occur at dusk and are termed dusk bat activity surveys by the Bat Conservation Trust 2012). While roost and automated surveys are covered by detailed protocols (Bat Conservation Trust 2007, 2012), the protocol for undertaking activity surveys using handheld ultrasonic detectors is less well defined and subject to confounding factors. For example, since it is rarely possible to undertake activity surveys through the entire night (as is recommended for automated surveys: Richards 2001), ensuring synchronicity between survey time and peak bat activity is vital. This can be difficult since: 1) most species have non-uniform nightly activity (typically showing a positively-skewed or bimodal activity pattern: Rydell et al. 1996, Hayes 1997); and 2) different species have different time-activity patterns due to relative predation risk, energy demands, and synchrony with different food resources, as well as for temporal niche

partitioning in multi-species guilds (Kunz 1973, Rydell et al. 1996, Duvergé et al. 2000, Russ 2012).

Activity surveys typically involve a surveyor walking a pre-defined transect at a constant pace carrying a bat detector and stopping at pre-defined listening points for a set time period (at least three min). Bat activity is recorded continually along the transect and at each point. At a European level, the only guidance on timing of surveys is that they should be consistent with respect to sunset and last 1–3 h (Battersby, 2010). In the UK, the Bat Conservation Trust (BCT) recently revised the dusk activity survey protocol for British bats (Bat Conservation Trust 2012) to become more prescriptive than previously (Bat Conservation Trust 2007). The new protocol recommends that dusk surveys should start 15–30 min before sunset and last around two hours (differing from the 2007 protocol when starting at sunset was recommended). The new protocol has been adopted by statutory regulators. In contrast, the main UK monitoring scheme – National Bat Monitoring Scheme (NBMP) – continues to suggest that surveys should commence at sunset. The BCT protocol also conflicts with the fact most species do not emerge until at least 30 min after sunset (Jones and Rydell 1994, Russ 2012).

The recommendation of starting to survey 15–30 min before sunset is not based on any empirical evidence as a comparison of bat activity survey data from the same site at different times has not been undertaken (Milne et al. 2004). Instead, start times are a ‘best guess’ based on emergence time data for a few individual species, which may not translate to the best time to survey multiple species (Walsh et al. 2004). In South Australia, Law et al. (1998) found bat activity to be concentrated in the hour after sunset and noted that even for the few species with activity that peaked later, there was still a “mini-peak” of recordable activity during this period. This, and similar studies in North America and elsewhere in Australia (Hayes 1997, Milne et al. 2004, Scanlon and Petit 2009), all used passive monitoring (i.e. automated data collection using a remote unit rather than walked activity transects) and were undertaken on non-European Chiropteran species communities. There are thus substantial knowledge gaps regarding the optimal timing of bat activity surveys in general, and for the UK/European guild in particular (Hutson et al. 2001). The only study seemingly undertaken on European bats is that of Downs and Racey (2007), where pipistrelle bats (*Pipistrellus* spp.) were monitored throughout the nights at several sites in Scotland at a single point in relation to time, site and weather – this was active in the sense the researcher was present but passive in the sense that only a single point was surveyed. There is a need for more evidence-informed guidelines on how to design optimal bat-detector surveys to ensure data are as accurate and robust as possible (Jones 2004, Walsh et al. 2004, Stahlschmidt and Brühl 2012).

In this study we compare bat activity at the same sites, on the same nights, for replicate transects at different times in relation to sunset to determine whether there is an optimal time to undertake dusk bat activity surveys. Given that the most recent survey protocol for British bats (Bat Conservation Trust 2012) recommended that dusk activity surveys start 30 min before sunset, we hypothesise that bat activity levels will be highest for surveys that start at this time and

then decline as survey start time (and thus finish time) gets later. We further hypothesise that this pattern to be most pronounced for species that emerge from roosts earliest, such as the noctule *Nyctalus noctule*. We also compare bat activity as recorded from the transect itself (transect data) and from the listening points (point data). Point and transect bat activity data have only been directly compared once previously in Germany (Stahlschmidt and Brühl 2012). Although based on just three points as part of a larger study, this suggested that more bat passes were recorded at points than on the transect itself, but that the precision of the activity estimates was lower. We test whether this is the same in the UK on a larger scale.

## Material and methods

Fieldwork was undertaken in June and July 2013 at four sites in Gloucestershire, UK, two adjacent sites characterised as high-quality bat habitat and two adjacent sites characterised as low-quality habitat (following Bat Conservation Trust 2012). The habitat at the high-quality (centred on 51°93'N, 02°03'E) was open deciduous woodland with scattered shrub and field layers, high hedgerow connectivity, and adjacent to tree-lined waterways. The low-quality sites (centred on 51°92'N, 02°09'E) were pastoral farmland with some hedgerows 2 m high but low hedgerow connectivity and isolated from both woodland and water. At each site, a 3 km transect was devised, which linked 10 listening points. Transects were walked three times per night. The first survey replicate started 30 min before sunset and finished 90 min after sunset following the Bat Conservation Trust (2012) protocol (henceforth the pre-sunset survey). The second replicate started at sunset and finished 2 h after sunset following the NBMP protocol (henceforth the sunset survey). The third replicate started 30 min after sunset (in accordance with the emergence times of the majority of bat species: Jones and Rydell 1994, Russ 2012) and finished 2.5 h after sunset (henceforth the post-sunset survey). In all cases, surveyors walked the same route and stopped at the same pre-defined listening points for 3 min. In total, 240 hours' of data were collected (6 h per night × 10 nights at each site × 4 sites). To avoid each site being sampled during a different part of the season, we rotated between sites on successive nights. Data were only collected when weather conditions were suitable (dry, minimal wind, temperature > 7°C) so the sampling period was largely not entirely continuous with 40 nights' of data being collected in a 52 night period. There was no issue with seasonal change in timing as all surveys were standardised relative to sunset.

Rather than each surveyor using a bat detector with an audio output and identifying bat species in the field by sound alone, data were recorded continually to compact flash cards using frequency division AnaBat SD2 bat detectors fitted with a broad spectrum microphone, as recommended by Johnson et al. (2002). The time of arrival and departure from each listening point was noted. Post-fieldwork, data were downloaded using CFCread and analysed using AnaloookW (ver. 3.9c) (<www.hoarybat.com/Beta>) so species could be identified using sonograms to improve accuracy (Walsh et al. 2004). Species-specific

Table 1. Results of linear mixed models analysing with two fixed factors: 1) survey replicate (data from pre-sunset versus sunset, versus post-sunset) and 2) transect data versus listening point data; survey night and site were included as random factors to account for the same sites being surveyed on multiple nights.

Dependent	Contrast	High-quality bat habitat (woodland)		Low-quality bat habitat (farmland)	
		Mean $\pm$ 95%CI	Linear mixed model	Mean $\pm$ 95%CI	Linear mixed model
Overall bat activity (total passes)	pre-sunset	1.80 $\pm$ 0.68	} $F_{2,57} = 11.674$ ; <b>p &lt; 0.001</b>	1.40 $\pm$ 0.58	} $F_{2,57} = 2.684$ ; <b>p = 0.029</b>
	sunset	3.35 $\pm$ 0.59		2.50 $\pm$ 0.66	
	post-sunset	3.55 $\pm$ 0.82	} $F_{1,59} = 3.525$ ; p = 0.075	2.20 $\pm$ 0.91	} $F_{1,59} = 3.985$ ; <b>p = 0.049</b>
	transect	2.67 $\pm$ 0.61		1.60 $\pm$ 0.47	
	point	3.13 $\pm$ 0.65		2.40 $\pm$ 0.69	
Bat species richness (number of species)	pre-sunset	1.10 $\pm$ 0.31	} $F_{2,57} = 5.775$ ; <b>p = 0.005</b>	0.45 $\pm$ 0.22	} $F_{2,57} = 5.089$ ; <b>p = 0.009</b>
	sunset	1.65 $\pm$ 0.26		1.45 $\pm$ 0.30	
	post-sunset	1.45 $\pm$ 0.30	} $F_{1,59} = 18.632$ ; <b>p &lt; 0.001</b>	2.00 $\pm$ 0.28	} $F_{1,59} = 7.555$ ; <b>p = 0.008</b>
	transect	1.20 $\pm$ 0.12		1.20 $\pm$ 0.32	
	point	1.60 $\pm$ 0.26		1.40 $\pm$ 0.34	
Common pipistrelle <i>Pipistrellus pipistrellus</i>	pre-sunset	1.25 $\pm$ 0.58	} $F_{2,57} = 16.654$ ; <b>p &lt; 0.001</b>	0.20 $\pm$ 0.18	} $F_{2,57} = 41.235$ ; <b>p &lt; 0.001</b>
	sunset	2.05 $\pm$ 0.48		0.75 $\pm$ 0.37	
	post-sunset	2.95 $\pm$ 0.66	} $F_{1,59} = 0.431$ ; p = 0.521	1.65 $\pm$ 0.41	} $F_{1,59} = 5.252$ ; <b>p = 0.029</b>
	transect	2.17 $\pm$ 0.54		0.70 $\pm$ 0.28	
	point	2.00 $\pm$ 0.52		1.03 $\pm$ 0.39	
Soprano pipistrelle <i>Pipistrellus pygmaeus</i>	pre-sunset	0.55 $\pm$ 0.30	} $F_{2,57} = 11.269$ ; <b>p &lt; 0.001</b>	None	} $F_{2,57} = 4.457$ ; <b>p = 0.016</b>
	sunset	1.25 $\pm$ 0.49		1.00 $\pm$ 0.15	
	post-sunset	0.35 $\pm$ 0.26	} $F_{1,59} = 23.728$ ; <b>p &lt; 0.001</b>	1.40 $\pm$ 0.19	} $F_{1,59} = 0.663$ ; p = 0.419
	transect	0.45 $\pm$ 0.24		0.77 $\pm$ 0.11	
	point	1.00 $\pm$ 0.36		0.83 $\pm$ 0.12	
Noctule <i>Nyctalus noctula</i>	pre-sunset	—	} $F_{2,57} = 16.426$ ; <b>p &lt; 0.001</b>	0.25 $\pm$ 0.19	} $F_{2,57} = 16.426$ ; <b>p &lt; 0.001</b>
	sunset	—		1.70 $\pm$ 0.62	
	post-sunset	—	} $F_{1,59} = 9.961$ ; <b>p = 0.003</b>	1.20 $\pm$ 0.39	} $F_{1,59} = 9.961$ ; <b>p = 0.003</b>
	transect	—		0.83 $\pm$ 0.34	
	point	—		1.27 $\pm$ 0.23	
Natterer's <i>Myotis nattereri</i>	pre-sunset	None	} $F_{2,57} = 4.660$ ; <b>p = 0.013</b>	—	} $F_{2,57} = 4.660$ ; <b>p = 0.013</b>
	sunset	0.50 $\pm$ 0.41		—	
	post-sunset	2.00 $\pm$ 0.18	} $F_{1,59} = 0.663$ ; p = 0.419	—	} $F_{1,59} = 0.663$ ; p = 0.419
	transect	0.67 $\pm$ 0.18		—	
	point	1.00 $\pm$ 0.36		—	

data were converted to the standard metric of the number of species-specific bat passes per hour (PPH) (as per Law et al. 1998, Walsh et al. 2004, Bat Conservation Trust 2012) both while walking (transect data) and from the listening points (point data). For this study, a bat pass was defined as a close sequence of three or more calls that increased in volume to a peak and then decreased again (as the bat came nearer to the detector and then flew away from it). All Analook analysis was done jointly by co-authors LD and LW for all transect replicates. This de-coupled identification from specific individual fieldworkers and ensured there was no potential for bias between transect replicates due to inter-observer differences in bat identification or the way bat passes were counted. Data from the two high-quality woodland sites, which were adjacent to one another, were extremely similar and were thus pooled for the purposes of analysis; the same approach was taken for the two adjacent low-quality farmland sites. Each dataset contained PPH for each species recorded and two summary variables: 1) bat species richness (number of different bat species recorded); and 2) overall bat activity (total PPH).

To establish whether there were differences in bat activity, a linear mixed modelling approach was used. Two fixed factors were included: 1) survey replicate (pre-sunset, sunset,

post-sunset) and 2) data type (transect or point); night and site were included as random factors. A hierarchical design was used with nested factors (night and site) since the same sites were surveyed on multiple nights. In total, 10 models were computed with the five dependent variables (overall bat activity, species richness, and activity of each specific species identified) each being analysed for both high-quality and low-quality habitat. Post hoc tests were calculated for the survey replicate factor using the Bonferroni method to control for family-wise error. All analyses were undertaken for each habitat using IBM SPSS ver. 21. Given that the focus here was on activity levels, and not occupancy/abundance, using linear mixed modelling was a valid analytical approach. However, it should be noted that the alternative approach of occupancy modelling (MacKenzie et al. 2002, Bled et al. 2013), which separates detectability from true occupancy, would be needed for monitoring purposes.

## Results

In total, there were 1184 individual bat passes from the four sites combined. Several species were identified: common pipistrelle *Pipistrellus pipistrellus* and soprano pipistrelle

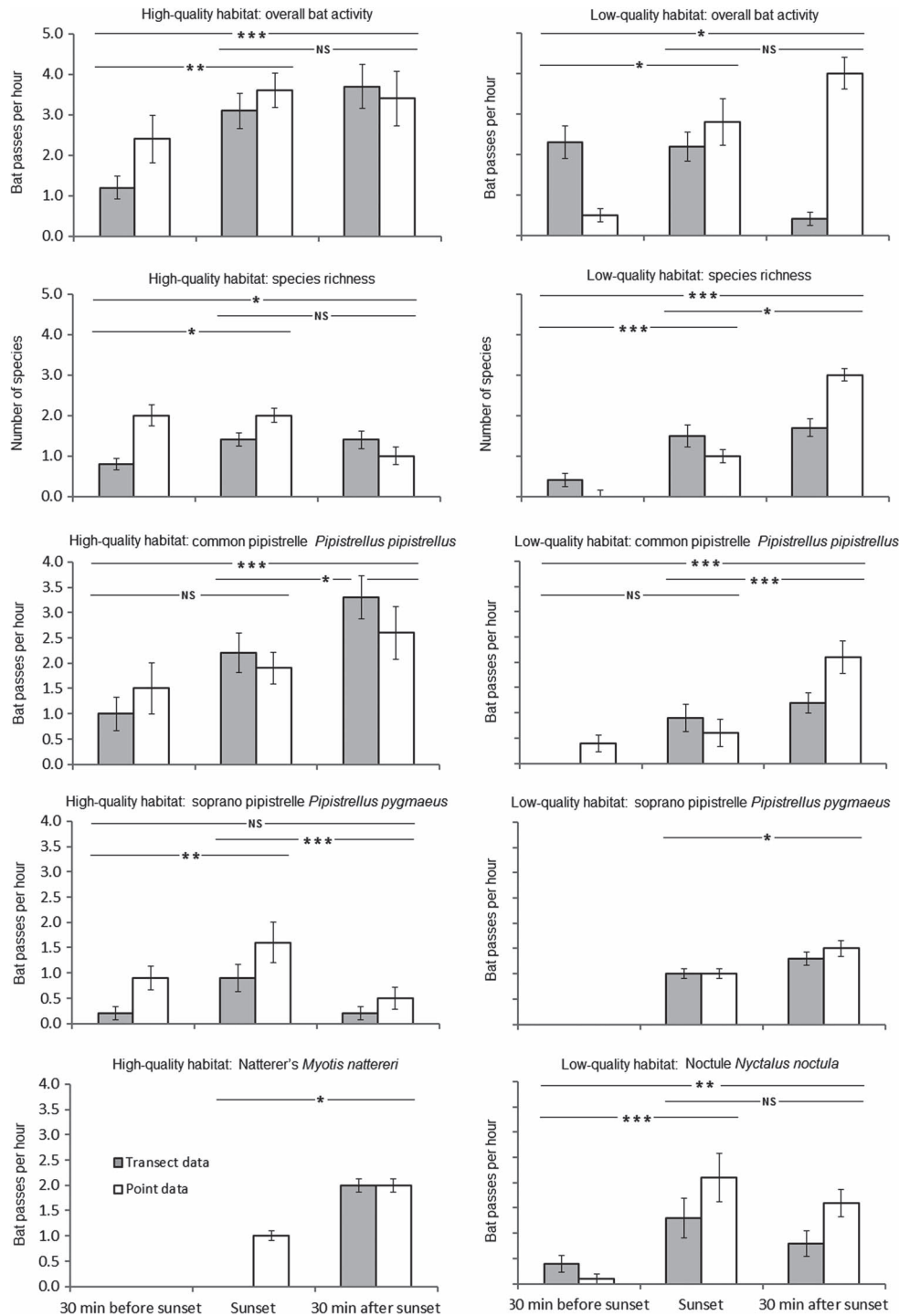


Figure 1. Bat activity recorded on two-hour bat activity walked transects and associated listening points three times per night with different start times at two different habitat types. Error bars show standard error. The significance of differences between the sampling periods is shown using asterisks (\* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; NS = non-significant).

*Pipistrellus pygmaeus* in both high- and low-quality habitat; Natterer's bat *Myotis nattereri* in high-quality woodland habitat and noctule *Nyctalus noctula* in low-quality open farmland habitat (Table 1, Fig. 1). All the species found are widespread across Europe.

Mean overall bat activity was 2.9 passes per hour (PPH) at the high-quality habitat (range 1.8–3.6 PPH depending on survey start time) and 2.0 PPH at the low-quality

open farmland habitat (range 1.4–2.5 PPH). All bat activity was higher for surveys that started at or after sunset relative to surveys that started pre-sunset (Table 1, Fig. 1). Overall bat activity was significantly higher for sunset and post-sunset surveys compared to pre-sunset surveys for both high-quality and low-quality habitat (post hoc  $p \leq 0.024$ ). Species richness was significantly higher for post-sunset surveys compared to sunset

(post hoc  $p = 0.014$ ) and pre-sunset surveys (post hoc  $p < 0.001$ ). In the high-quality habitat, the sunset and post-sunset surveys did not differ themselves but both were significantly (post hoc  $p \leq 0.021$ ) better than pre-sunset surveys.

These patterns were similar for the four individual species (Table 1, Fig. 1). For common pipistrelle, recorded activity was significantly (post hoc  $p \leq 0.038$ ) higher on post-sunset surveys compared to other survey times (low-quality habitat: mean = 1.7 PPH versus 0.5 PPH; high-quality habitat: mean = 3.0 PPH versus 1.7 PPH). For soprano pipistrelle, activity was significantly (post hoc  $p \leq 0.011$ ) higher on sunset surveys compared to other survey times for high-quality habitat (mean = 1.3 PPH versus 0.5 PPH). For the low-quality habitat for this species, activity on sunset post-survey was significantly higher (post hoc  $p = 0.034$ ) than sunset surveys (1.0 PPH versus 1.4 PPH); no passes were recorded on the pre-sunset survey. Noctules were only recorded in low-quality habitat, where activity was significantly higher on sunset and post-sunset surveys (mean 1.5 PPH) compared to pre-sunset surveys (0.3 PPH) (post hoc  $p \leq 0.003$ ). Natterer's were only recorded in the high-quality habitat and activity was significantly higher (post hoc  $p = 0.049$ ) on post-sunset surveys (2.0 PPH) than sunset surveys (0.5 PPH); no passes were recorded on the pre-sunset survey.

All bat species recorded at a given site were represented in both point and transect data. The only exceptions for specific survey replicates were common pipistrelle in low-quality habitat (point data only on the pre-sunset survey) and Natterer's (point data only on the sunset survey). There were several significant differences between point and transect data, with point data yielding higher estimates of: 1) overall activity in low-quality habitat; 2) bat species richness in both high- and low-quality habitat; 3) common pipistrelle activity in low-quality habitat; 4) noctule activity in low-quality habitats; and 5) soprano pipistrelle in high-quality habitat (Table 1, Fig. 1).

## Discussion

This study is the first to compare data from multiple dusk bat activity surveys at the same sites on the same nights empirically. It has shown that in the UK surveys starting before sunset (as per Bat Conservation Trust 2012 guidelines) record lower bat activity than surveys that start at sunset or 30 min after sunset in both high-quality woodland and low-quality open farmland habitats. This is contrary to our hypothesis that bat activity would decrease as start time (and thus finish time) became later. This was based on the fact that peak activity was the first hour after sunset in rural settings in Australia using passive techniques (Law et al. 1998) and underlines the need to establish the optimal survey time empirically for each Chiropteran species community.

In our study, fewer species were detected in low-quality habitat on pre-sunset surveys relative to sunset and post-sunset surveys due to the complete absence of soprano pipistrelle and the very low occurrence of noctule in the pre-sunset surveys in this habitat. However, recording the two-hour period following sunset allowed all species to be recorded in both high- and low-quality habitats. This agrees

with North America and north Australia, where the two-hour period following sunset allowed most species present to be recorded on most nights (Hayes 1997, Milne et al. 2004).

The species identified here are widespread across Europe. Findings here agree with the only work on European species published previously: a study of common and soprano pipistrelles in Scotland (Downs and Racey 2007). That study, which focussed on the effect of weather and temperature on different types of bat calls rather than optimal survey time specifically, found orientation calls of both species increased in 45 minute blocks after sunset peaking in block 3 (1 h 30 min – 2 h 15 min after sunset). In our study, common and soprano pipistrelle activity was generally recorded in the post-sunset survey (the exception being soprano pipistrelle in high-quality habitat where the sunset survey was best which was 30 min – 2 h 15 min after sunset). Somewhat surprisingly, noctule bat activity was very low on pre-sunset surveys and increased in sunset and post-sunset surveys. This was completely the opposite of what we had hypothesised on the basis that the noctule is the UK species with the earliest emergence (Russ 2012) and is one of the earliest-emerging bats in Europe (Jones and Rydell, 1994).

Generally findings were fairly similar for the different habitats. The main species-specific exception was soprano pipistrelle: the sunset survey was best in high-quality habitat whereas the post-sunset survey was best in low-quality habitat. This might be because the high-quality habitat was wooded and the presence of canopy meant ambient light levels decreased more quickly after sunset relative to low-quality sites characterised by open farmland. This underlines the possible need to amend survey protocols in different landscapes, even when surveying the same species. This was also seen in Australia where activity peaks more than 2 h after sunset (Scanlon and Petit 2009) in urban environments versus the first hour after sunset in rural settings (Law et al. 1998). This might be due to the effects of artificial lighting affecting foraging behaviour due to light-dependent predation risk (Stone et al. 2009) or more complex diurnal-nocturnal niche partitioning with other taxa.

Point and transect data have only been directly compared once previously (Stahlschmidt and Brühl 2012), when activity based on point data was found to both higher and less variable than transect data. Our findings partly agree: bat activity was generally higher at points (significantly so in low-quality habitat only) and species richness was significantly greater at points in both low- and high-quality habitat. This was driven by point activity data being higher for specific species (common pipistrelle and noctule activity in low-quality habitat; soprano pipistrelle in high-quality habitat). However, variability was lower (Table 1). On no occasion was a species represented in only point or transect data. Listening points are therefore vital but walking data are still valuable and can be collected with little effort while moving between points. We thus agree with the EUROBATS Guidelines for Surveillance and Monitoring of European Bats (Battersby 2010) that bat activity survey protocols combine the advantages of transect sampling (good site coverage and quick to undertake: Walsh et al. 2001) and point sampling (can be strategically placed: Verboom 1998, Stahlschmidt and Brühl 2012).

It is recognised that our study has not surveyed all species in the UK guild, and only a very small part of the European guild. We recommend that more multi-transect-per-night bat activity survey data be collected from across the UK, and in other countries for other Chiropteran guilds, to establish the generality of these findings. In the meantime, we recommended that two-hour dusk bat activity surveys start at or after sunset rather than 30 min before sunset (for three-hour surveys, starting at sunset is recommended) and continue to combine listening point data and data obtained while walking between points.

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## References

- Bat Conservation Trust 2007. Bat surveys: good practice guidelines. – Bat Conservation Trust.
- Bat Conservation Trust 2012. Bat surveys: good practice guidelines, 2nd edn. – Bat Conservation Trust.
- Battersby, J. 2010. Guidelines for surveillance and monitoring of European Bats. – EUROBAT'S Publ. no. 5.
- Bled, F. et al. 2013. Modeling trends from North American breeding bird survey data: a spatially explicit approach. – *PLoS ONE*. 8: e81867.
- Downs, N. C. and Racey, P. A. 2007. Temporal and spatial differences in the emission of calls by pipistrelle bats *Pipistrellus pipistrellus* and *P. pygmaeus*. – *Acta Theriol.* 52: 55–64.
- Duvergé, P. L. et al. 2000. Functional significance of emergence timing in bats. – *Ecography* 23: 32–40.
- European Environment Agency 2013. European bat population trends: a prototype biodiversity indicator. – EEA Tech. Rep. 19/2013.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. – *J. Mammal.* 78: 514–524.
- Hutson, A. M. et al. 2001. Microchiropteran bats: global status survey and conservation action plan – IUCN/SSC Chiroptera Specialist Group, IUCN.
- Johnson, J. B. et al. 2002. A comparison of two acoustical bat survey techniques. – *Wildl. Soc. Bull.* 30: 931–936.
- Jones, G. 2004. Where do we go from here? – In: Brigham, R. M. et al. (eds), *Bat echolocation research: tools, techniques and analysis*. *Bat Conserv. Int.*, pp. 166–167.
- Jones, G. and Rydell, J. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. – *Phil. Trans. R. Soc. B.* 346: 445–455.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. – *J. Mammal.* 54:14–32.
- Lacki, M. J. et al. 2007. *Bats in forests: conservation and management*. – John Hopkins Univ. Press.
- Law, B. et al. 1998. A bat survey in state forests on the south-west slopes region of New South Wales with suggestions of improvements for future surveys. – *Aust. Zool.* 30: 467–479.
- MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – *Ecology* 83: 2248–2255.
- Milne, D. J. et al. 2004. A comparison of three survey methods for collecting bat echolocation calls and species-accumulation rates from nightly *Anabat* recordings. – *Wildl. Res.* 31: 57–63.
- Racey, P. A. and Entwistle, A. C. 2005. Conservation ecology of bats. – In: Kunz, T. H. and Fenton, M. B. (eds), *Bat ecology*. Univ. of Chicago Press, pp. 680–744.
- Richards, G. C. 2001. Towards defining adequate bat survey methodology: why electronic call detection is essential throughout the night. – *Aust. Bat Soc. Newslett.* 16: 24–28.
- Russ, J. 2012. *British bat calls: a guide to species identification*. – Pelagic Publishing.
- Rydell, J. et al. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. – *Oikos* 76: 243–252.
- Scanlon, A. T. and Petit, S. 2009. Effects of site, time, weather and light on urban bat activity and richness: considerations for survey effort. – *Wildl. Res.* 35: 821–834.
- Stahlschmidt, P. and Brühl, C. A. 2012. Bats as bioindicators – the need of a standardized method for acoustic bat activity surveys. – *Meth. Ecol. Evol.* 3: 503–508.
- Stone, E. L. et al. 2009. Street lighting disturbs commuting bats. – *Curr. Biol.* 19: 1123–1127.
- Verboom, B. 1998. The use of edge habitats by commuting and foraging bats. – DLO Inst. For. Nat. Res., the Netherlands.
- Walsh, A. L. et al. 2001. The UK's national bat monitoring programme. – DEFRA Final Report, London.
- Walsh, A. L. et al. 2004. Designing bat-activity surveys for inventory and monitoring studies at local and regional scales. – In: Brigham, R. M. et al. (eds), *Bat echolocation research: tools, techniques and analysis*. *Bat Conserv. Int.*, pp. 157–166.