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Abiotic and spatiotemporal factors affect activity of European bat species and have implications for detectability for acoustic surveys

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Bat activity surveys are essential in the contexts of scientific research, conservation, assessment of ecosystem health, monitoring progress towards sustainable development goals, and legislative compliance in development and infrastructure construction. However, environmental conditions have the potential to influence bat activity and, in turn, their detectability in acoustic surveys. Here we use 3242 hours of acoustic survey data from 323 nights of bat monitoring at 14 sites over a 4-year period to explore the influence of spatiotemporal factors, lunar phase and weather conditions on bat activity. All spatiotemporal and abiotic factors analysed (site, hour post sunset, length of night, duration of moonlight, temperature, rain, wind and cloud cover) contributed to the optimal multivariate model for at least one bat species/genus; all factors except cloud cover and temperature were significant in the optimal model for total bat activity. However, there were notable species-specific differences. Among the key findings were differences between *Pipistrellus* species, with periods of rainfall being negatively related to soprano pipistrelle *Pipistrellus pygmaeus* registrations but not those of common pipistrelle *Pipistrellus pipistrellus*. In addition, overcast conditions showed a strong positive relationship with the number of *Myotis* registrations while duration of moonlight was positively correlated with common pipistrelle. Temperature was only important for *Nyctalus* species. These findings demonstrate that understanding the effect multifaceted and interlinked environmental factors on the activity of different bat species is a vital step in developing maximally effective survey protocols, which, in turn, will improve the reliability of conservation and planning decisions underpinned by survey data.

Keywords: anabat, automated surveys, bat surveying, echolocation, monitoring, ultrasonic detection

Bats (Chiroptera) are the second largest mammalian order with 1100 species worldwide (Kunz and Lumsden 2003, Simmons et al. 2008). They have diversified over the past 52 million years to inhabit numerous habitats and utilise a range of food sources and foraging techniques (Patterson et al. 2003). Insectivorous species, such as those found in Europe, are nocturnal and typically use echolocation to catch prey by aerial hawking (e.g. *Pipistrellus*) or from the surface of water (e.g. *Myotis*), as well as for navigation.

Although the broad-scale biogeographical ranges of most species are widely documented, and habitat requirements are reasonably well understood, at least for roost sites, there remain considerable gaps in knowledge regarding the factors that influence local-scale foraging activity both spatially and temporally (Barclay 1991, Walsh and Harris 1996a, b, Erickson and West 2002, Ciechanowski et al. 2007). Given that acoustic bat surveys depend on detecting echolocation during foraging (and when bats are commuting between roost and feeding grounds), understanding the spatiotemporal and abiotic factors that influence detection is key to obtaining robust survey data (Hayes 1997). This is of particular importance given the use of bat surveys in conservation contexts (Barlow et al. 2015) and to quantify ecosystem health (Jones et al. 2009), as well as when surveys of legally-protected species are a statutory obligation in infrastructure and development planning (Collins 2016). In Europe, bats are protected under the European Protected Species licensing framework to ensure compliance with the EC Habitats Directive (92/43/EEC), with countries implementing this via their own national legislation (e.g. Wildlife and Countryside Act 1981 and Conservation of Habitats and Species Regulations 2010 in the UK).

Bats are not spatially uniform in occurrence. Habitat suitability for foraging is largely determined by insect prevalence and foraging opportunities. High-quality foraging habitat includes broadleaf woodland, water and linear vegetation corridors (Walsh and Harris 1996a) whereas arable land and improved grassland are generally less favoured

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(Walsh and Harris 1996b). Some species have particular habitat requirements for foraging. For example, Daubenton's bats *Myotis daubentonii* forage over water (Rydell et al. 1999, Russ 2012), greater horseshoe bats *Rhinolophus ferrumequinum* are often associated with cattle (Ransome 1996), while brown long-eared bats *Plecotus auritus* depend on areas where there is suitable vegetation for gleaning (Rydell 1989a, Anderson and Racey 1991). Distribution of foraging sites also fundamentally depends on the location of roost sites and the distance individuals commute to their feeding grounds. For British bats, commuting distance can range from as little as < 1 km (e.g. Bechstein's bat *Myotis bechsteinii*) to up to 14 km (e.g. Leisler's bat *Nyctalus leisleri*) (Hundt 2012).

Temporal factors can also affect bat foraging and feeding behaviour, and thus their detection on bat surveys. Seasonality affects the presence of foraging temperate bats as they typically hibernate overwinter or migrate to other areas. Females are most active in early summer due to the high energy demands of pregnancy and lactation (Racey and Speakman 1987, Ciechanowski et al. 2007). Late in the summer, young bats increase the size of the population foraging (Erickson and West 2002). This, together with the fact that adults often spend more time away from the roost after weaning, typically increases observed activity levels from late July to September (Maier 1992). Different bat species also have different circadian rhythms and emerge at different times post-sunset (Jones and Rydell 1994) both relative to one another and potentially also in response to night duration.

Abiotic factors also have the potential to affect bat activity and thus detectability in acoustic surveys. Light levels, including moonlight duration and intensity, could be especially important. A global meta-analysis by Saldaña-Vázquez and Munguía-Rosas (2013) combined results of multiple studies to research the effects of moonlight on bats. Their analyses found a significant negative relationship between moonlight intensity and levels of bat activity, indicating that some species were lunar phobic. The strongest effect was found in tropical frugivorous species, for example Neotropical fruit bats (*Artibeus*) (Morrison 1978), and in Neotropical species that forage over water, such as the greater bulldog bat *Noctilio leporinus* (Börk 2006). The limited research on the effect of moonlight on insectivorous bats in at higher latitudes is less conclusive. Negraeff and Brigham (1995) found no indication of lunar-phobic behaviour based on work in Canada. This is possibly because bats at higher latitudes have lower nocturnal predation risk than those in the tropics (Karlsson et al. 2002). However, even if predation pressures in temperate bats are low, there remains the potential for impacts on emergence times and bat activity patterns, both spatially and temporally (Lima and O'Keefe 2013). In the Pacific northwest, Erickson and West (2002) suggested that variation in insectivorous bat activity might relate to moonlight intensity but did not explicitly test this hypothesis. The phenomenon has not been extensively studied for European species. Weather conditions can also influence bat activity. As small, endothermic mammals, bats use a large proportion of their energy to thermoregulate (Lewis 1993). Lower air temperatures and rainfall require the bats to utilise more energy to maintain suitable body temperature, such that foraging in these conditions may be unfavourable. Insect prey may also be less abundant in poor weather (Racey and Speakman 1987). Although weather conditions can cause bat activity to differ substantially on consecutive nights (Hayes 1997), it does not account for all within- or between-night variation. Moreover, a study by Erickson and West (2002) showed that rain and temperatures accounted for 37% of the variation in insectivorous bat activity.

Here we explore the influence of spatiotemporal and abiotic variables on bat activity using data from automated monitoring from 14 sites over a four-year period (3242 survey hours over 323 nights). This encompassed both overall bat activity, as well as species- and genus-specific trends in relation to site, nocturnal emergence patterns, duration of moonlight and weather variables. Understanding the effect of these multifaceted and interlinked factors on the activity of different bat species is a vital step in ultimately developing maximally effective survey protocols, which, in turn, will improve the reliability of conservation and planning decisions made using survey data.

Material and methods

Data collection

Data were collected between 2014 and 2017 across 14 sites in the south of England. The sites represented a range of habitat types. Most of the sites (n = 9) comprised agricultural land with dividing hedgerows. The remaining sites were rural sites with heterogeneous habitat including well established treelines, woodland, and/or watercourses (n = 3), or were green spaces within urban areas (n = 2). An Anabat Express bat detector unit (Titley Scientific, Ballina, Australia) was deployed at the study sites in rotation to record data across the sites for a total of 323 nights between sunset and sunrise. Deployment and positioning was carried out in a consistent manner at all sites with units mounted about 1.75 m above the ground adjacent to a suitable hedgerow or treeline to ensure detection of commuting and foraging activity along linear features. The units recorded data directly onto an SD card.

Post fieldwork, all data from the bat detectors were downloaded for sonogram analysis. The analysis was performed in AnalookW software (Titley Scientific, Ballina, Australia) developed specifically for Anabat detectors. Initially recordings were processed on a night-by-night basis and then data were subdivided into hourly units relative to sunset. This gave a total of 3424 hours of survey data over 323 nights, with each night of data being from a single site (i.e. sites were sampled independently not concurrently). Survey effort (number of survey nights per month and per site) is given in Supplementary material Appendix 1 Table A1. Species identification was carried out by assessment of the range and peak frequency, together with shape of each sonogram in terms of pitch and amplitude over time (Russ 2012).

Data relating to temporal and abiotic factors were collected for use as explanatory factors in statistical modelling. The variables are explained in Table 1. Sunset, sunrise and lunar data were taken from time and date AS (<www.timeanddate.com>). Weather data were obtained via BBC

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Table 1. Temporal and abiotic data collected for use in statistical analyses. All data were hourly (n = 3242).

Name	Details	Data type
Time post sunset	Bat survey hour relative to sunset, whereby 1 was the first hour post sunset, 2 was the second hour post sunset etc. The number of full survey hours varied between 08:00 and 14:00 depending on the length of night, with a modal duration of 10 h.	continuous
Illumination	Illumination based on moon presence taking into account moonrise and moonset times, as well as cloud cover. Note that depending on the lunar phase, on some nights moonrise was at/before sunset (such that potential moonlight was at the start of the night) but that on other nights moonrise was after sunset (such that there was no potential moonlight for the first part of the night). The moon was potentially present for part of the night on all survey nights. Lunar timing information was combined with hourly cloud cover to give a ranking scale whereby: 0 = no illumination (no moon present for any part of the survey hour and/or overcast skies; 56.9% of cases); 0.5 = partial illumination (moon present for part of the hour only and/or patchy cloud; 30.3% of cases); and 1 = full illumination (moon present for full survey hour and clear skies; 12.8% of cases). None of the 14 survey sites was subject to artificial illumination.	categorical
Temperature	Measured in degrees Celsius (°C). Min = 1°C; max = 27°C; mean = 13.2°C	continuous
Wind speed	Average miles per hour (mph). Min = 0 mph, max = 30 mph; mean = 7 mph.	continuous
Rainfall	Ranking scale of: 1 = none (63.4% of cases), 2 = intermittent and/or light (18.6% of cases), 3 = persistent and/or heavy (18.0% of cases).	categorical

(<www.bbc.co.uk/weather>) for the nearest town or using time and date AS using the nearest available weather station.

Statistical analysis

To examine whether there were significant deviations from a uniform distribution of bat registrations throughout the night, Kolmogorov–Smirnov two-sample tests were used as per Milne et al. (2005) for Australian bat species.

To explore the influence of spatiotemporal and abiotic factors on bat activity, generalised linear mixed models (GLMMs) were constructed. Models were developed for overall bat activity (total number of bat passes per hour regardless of species: n = 3424) and also the activity of each of the four most prevalent species/genus groups; common pipistrelle *Pipistrellus pipistrellus*, soprano pipistrelle *Pipistrellus pygmaeus*, *Myotis* spp. and *Nyctalus* spp. (specific bat passes per hour: n = 3424). In all cases, a full model was constructed whereby the factors listed in Table 1 were entered as continuous fixed factors (hour post sunset, temperature, wind speed) or categorical fixed factors (illumination, rainfall). Two random factors were also entered: site (coded 1–14 with no underlying rationale for the order and thus entered as a categorical random factor) and month (April–October). Because the dependent variable of bat activity (total or species-specific) used count data (number of bat passes per hour), a Poisson distribution was used with a log link function: this gave the lowest Akaike's information criterion (AIC) value (Akaike 1971) relative to other options for count data of Poisson with identity link, negative binomial with log link, and negative binomial with identity link. For the random factors, a scaled identity covariance type was specified as this covariance structure was associated with the lowest AIC score. To ascertain the effect of the fixed factors in explaining bat activity, marginal r^2 was calculated. To ascertain the effect of both fixed and random factors, conditional r^2 was calculated. The relative importance of the random factors can be inferred from the difference between conditional and marginal r^2.

Once full models had been computed for bat activity, reduced models were tested by dropping different combinations of fixed factors to establish whether the full model was optimal or whether a simpler model might better balance explanatory power and parsimony. Competing models were compared using delta (Δ) AIC on the basis that models with $\Delta AIC \leq 2$ had essentially have the same support and models with ΔAIC of 3–4 had strong support; models with $AIC \geq 5$ were considered to have substantially less support and were discounted (Burnham and Anderson 2002). In all cases the full model was optimal and hence only full models are reported. All statistical analysis was carried out in IBM SPSS Statistics ver. 24.

Results

In total, 52 628 bat registrations were recorded over 3242 survey hours between sunset and sunrise across 323 nights. The majority of registrations were: common pipistrelle = 29 657, soprano pipistrelle = 13 034, *Myotis* spp. = 7146 and *Nyctalus* spp. = 831. The remaining 1960 registrations were split between serotine *Eptesicus serotinus*, brown long-eared *Plecotus auritus*, greater horseshoe *Rhinolophus ferrumequinum*, lesser horseshoe *Rhinolophus hipposideros*, barbastelle *Barbastella barbastellus* bats: these species were encountered too infrequently for meaningful statistical analysis. As common pipistrelle or soprano pipistrelle overlap in call frequency, there were also some *Pipistrellus* calls between 50 and 51 kHz that could not be definitively identified. As per Russ (2012), we classified *Pipistrellus* calls with a maximum energy (peak) frequency < 50.2 kHz as common pipistrelle and *Pipistrellus* calls with a maximum energy (peak) frequency > 50.6 kHz as soprano pipistrelle, while those between 50.2 and 50.6 were discounted from analysis unless they were part of a series of calls that had already been identified definitively to species level. The mean number of bat passes per hour for total activity and the four specific taxa are given in Supplementary material Appendix 1 Table A1 on a per month, per site basis.

Temporal distribution

Two sample Kolmogorov–Smirnov tests demonstrated that registrations of all species/genera differed significantly from

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a uniform distribution ($p \leq 0.046$ in all cases). The majority of bat registrations, regardless of species, occurred in the first hour post sunset and then decreased as the night progressed, with a small increase in activity towards dawn that made the overall activity distribution slightly bimodal (Fig. 1a). Both pipistrelle species also showed higher activity in the hours immediately following sunset (Fig. 1b–c), however, soprano pipistrelle alone showed an additional peak in activity towards dawn (Fig. 1c). The temporal distribution of *Nyctalus* registrations (Fig. 1d) was the most sporadic, with higher peaks in activity occurring haphazardly throughout the night. However, this species was recorded much less

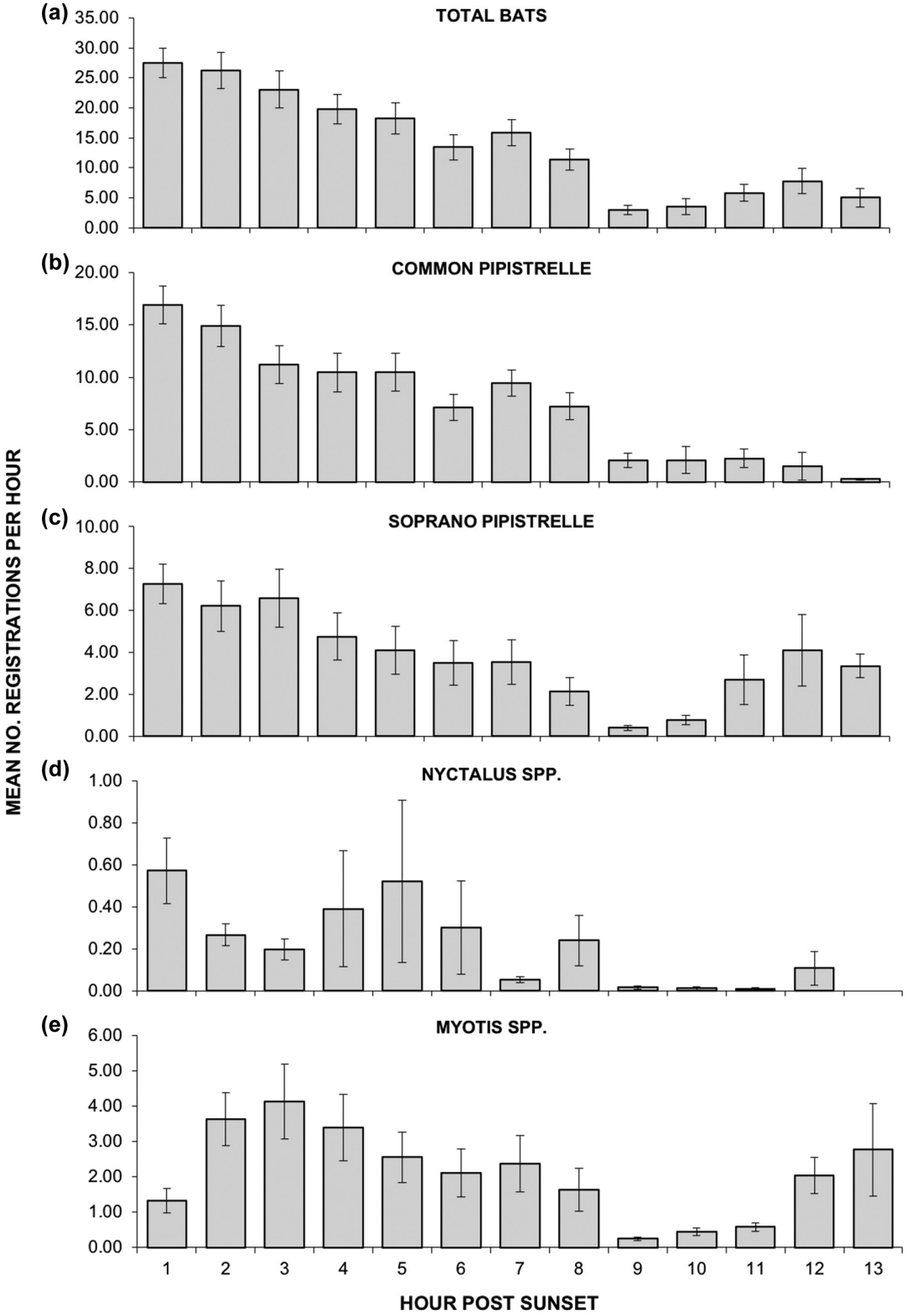


Figure 1. Mean number of registrations in each hour post sunset for total bats and within species/genus. Error bars show the standard error.

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Table 2. Generalized linear mixed models exploring the influence of temporal and abiotic factors on overall bat activity (bat passes per hour) and activity for four specific taxa (n = 3242 survey hours across a total of 323 nights and 14 sites). The models used a Poisson distribution with a log link function. For the three continuous fixed factors – hour post sunset, temperature and wind speed – the gradient of any significant relationship with bat activity is given with the standard error below in parentheses. For the two fixed factors – illumination and rainfall – the estimated marginal mean (EMM) is given with the standard error below in parentheses. In all models, site (n = 14) and month (n = 7) were included as random factors. The importance of the fixed factors in explaining bat activity can be assessed using the marginal r squared value (r^2_m), while the additional importance of the random factors can be assessed using the difference between r^2_m and the conditional r squared value (r^2_c). For more details of the variables, including the categories for illumination and rainfall, please see Table 1.

	Overall model		Hour post sunset			Temperature			Wind speed			Illumination				Rainfall			
	r^2_m	r^2_c	F	p	Gradient	F	p	Gradient	F	p	Gradient	F	p	EMM none	EMM partial	EMM full	F	p	EMM none	EMM light	EMM heavy
Total activity	0.369	0.474	6798	<0.001	−0.147 (0.002)	61	<0.001	0.015 (0.002)	2822	<0.001	0.067 (0.001)	208	<0.001	4.838 (0.054)	4.002 (0.044)	2.934 (0.044)	393	<0.001	5.668 (0.063)	5.114 (0.057)	2.628 (0.029)
Common pipistrelle	0.286	0.347	2986	<0.001	−0.176 (0.002)	78	<0.001	0.022 (0.003)	2402	<0.001	0.071 (0.002)	18	<0.001	2.390 (0.030)	2.222 (0.032)	2.203 (0.032)	71	<0.001	2.791 (0.040)	2.614 (0.038)	1.606 (0.023)
Soprano pipistrelle	0.423	0.478	2406	<0.001	−0.133 (0.004)	1	0.592	N/A	589	<0.001	0.065 (0.003)	128	<0.001	0.214 (0.006)	0.163 (0.005)	0.127 (0.004)	314	<0.001	0.280 (0.009)	0.257 (0.009)	0.062 (0.002)
Myotis spp.	0.282	0.513	962	<0.001	−0.133 (0.005)	20	<0.001	−0.029 (0.006)	322	<0.001	0.067 (0.004)	57	<0.001	0.131 (0.005)	0.096 (0.003)	0.120 (0.004)	29	<0.001	0.139 (0.005)	0.109 (0.004)	0.100 (0.004)
Nyctalus spp.	0.354	0.357	11	0	−0.051 (0.015)	518	<0.001	0.383 (0.017)	111	<0.001	−0.111 (0.011)	4	0.020	0.055 (0.002)	0.068 (0.003)	0.053 (0.002)	13	<0.001	0.117 (0.005)	0.043 (0.002)	0.040 (0.002)

frequently than pipistrelle species or *Myotis* spp. and thus the variability in registrations, as shown by the standard error bars, was considerably higher. *Myotis* registrations were relatively infrequent in the first hour post sunset (Fig. 1e), but increased thereafter, peaking in the third hour post sunset and then decreasing, with a small peak in activity prior to dawn.

Spatiotemporal and abiotic influences on bat activity

Hour post sunset, temperature, wind speed, illumination and rainfall all had a significant effect on overall bat activity (bat passes per hour regardless of species) and the activity of the four focal taxa; the single exception was temperature for soprano pipistrelle, which was not significant (Table 2).

Hour post sunset was significantly negatively related to overall bat activity: bat passes per hour decreased by 0.147 per hour (± 0.002 SEM) as the night progressed. Similar negative relationships were seen for activity in all four specific taxa, with gradients varying between -0.051 ± 0.017 (*Nyctalus*) and -0.176 ± 0.004 (common pipistrelle). These relationships largely reflect the temporal pattern of bat activity decreasing throughout the night (Fig. 1), with the shallower gradients being for species with a notable pre-dawn peak in activity (soprano pipistrelle) or species whose activity was sporadic throughout the night (*Nyctalus*).

The relationship between temperature and overall bat activity was weakly positive, with bat activity increasing by 0.015 bat passes per hour (± 0.002 SEM) for each °C increase in temperature. A similar pattern was seen for common pipistrelle (0.022 ± 0.003), with a stronger positive relationship being found for *Nyctalus* (0.383 ± 0.017). A weak negative relationship was observed between temperature and *Myotis* (-0.029 ± 0.006). There was a significant positive relationship between bat activity and wind speed for overall bat activity and for activity of common pipistrelle, soprano pipistrelle and *Myotis*: all relationships were comparatively similar with bat passes per hour increasing by ~0.067 (± ~0.002 SEM) for each additional mile per hour in wind speed. The exception was *Nyctalus* where bat passes decreased by 0.111 (± 0.011 SEM) for each additional mph in wind speed. Bat activity, both overall and for each of the four focal taxa, was significantly lower in heavy rain. In the case of overall activity, bat passes per hour were fairly consistent in dry conditions and in light rain (5.668 and 5.114 bat passes per hour, respectively), but decreased substantially in heavy rain (2.628 bat passes per hour). This notable decrease in activity in heavy rain also occurred for both pipistrelle species. In contrast, *Myotis* declined linearly as rain intensified, while *Nyctalus* activity dropped substantially between dry conditions and light rain with activity levels light and heavy rain being approximately equal.

The impact of moon illumination on bat activity was more varied between taxa. Overall bat activity was significantly lower in instances of full illumination (2.934 bat passes per hour), than in partial or no illumination (4.002 and 4.838, respectively). The effect of moonlight on activity of both common and soprano pipistrelle was more gradual but remained negative. The effect on moonlight on *Nyctalus* and *Myotis* bats was less clear: partial illumination was associated with peak activity of *Nyctalus* and lowest activity of *Myotis*.

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The random factors of site and month increased the amount of variance in total bat activity explained by the GLMM ($r^2_m = 0.369$ versus $r^2_c = 0.474$; a difference of 0.105). This demonstrates the importance of site-specific factors and seasonality on overall bat activity. For specific taxa, site and month varied in how much they influenced bat activity, with the difference between conditional and marginal r^2 values being negligible for *Nyctalus* (0.003) and low for soprano and common pipistrelle (0.055 and 0.061, respectively), but substantially higher for *Myotis* (0.231). It is important to note that the fixed factors (hour post sunset, temperature, wind speed, illumination and rainfall) together accounted for substantially more variation in bat activity than did the random factors of site and month in all cases.

Discussion

Spatiotemporal factors

Bat populations differ across time and space suggesting that resource partitioning is important in facilitating the co-existence of multiple species (Arlettaz 1999). Within the United Kingdom, such partitioning has been observed previously between Pipistrelle species, which differ in foraging locations and feeding times (Nicholls and Racey 2006). Here, we found that random factors of site and month typically accounted for 12–22% of the variation in bat activity but were particularly important for *Myotis*, where they accounted for 45% of the variation explained by the GLMM model. This is likely driven by Daubenton's bats *Myotis daubentonii*, which are associated with water as they glean insect prey from the surface of lakes and ponds (Jones and Rayner 1988, Russ 2012) and were thus present in large numbers at some sites and absent from others. Seasonality (accounted for here by adding month as a random factor) is also likely to impact observed levels of activity. Temperate bats in the United Kingdom are most active during the summer months, foraging regularly to prepare for, or to recover from, the high energy demands of raising young (Racey and Speakman 1987, Ciechanowski et al. 2007). All bats remain active for the remainder of the summer and into early autumn to ensure they have sufficient energy reserves for winter hibernation (Speakman and Racey 1989). The time at which bats enter and emerge from hibernation is primarily dependent on temperature. They enter torpor when energy demands are higher than can be met by decreasing insect densities (Speakman and Racey 1989). Depending on ambient temperature, bats typically become active in April and seek out hibernation sites in late September as temperatures drop.

Bat activity was not uniform throughout the night, as shown by the clear patterns in the temporal distribution of activity across the night and reinforced by hour post sunset being significant in each GLMM. Bats emerge at different times (Russ 2012) and also commute different distances, at different speeds, between roosts and foraging areas. Some bats return to their roost part way through the night and then re-emerge for a pre-dawn feed and this likely explains the increase in bat activity shown towards sunrise shown here for soprano pipistrelle and *Myotis*. This has been seen to vary between nights and seasons (Anthony et al. 1981) and may be influenced by peaks insect densities at dusk and, to a lesser extent, at dawn (Rydell et al. 1996). Ultimately different temporal patterns in activity levels between species, as demonstrated here, plays an important role in niche partitioning in multi-species assemblages of insectivorous bats (Milne et al. 2005, Ciechanowski et al. 2007).

Weather

Temperature was weakly positively correlated with bat activity both overall and for common pipistrelle (i.e. more registrations in warmer conditions). This was expected given that bat activity tends to peak in the summer months, when temperatures are usually highest. The weak negative relationship between temperature and bat activity for *Myotis* and *Nyctalus* was more surprising. However, as surveys were undertaken between April and early October, when it is typically warm enough for bats and their insect prey to be active, one explanation is that temperature is important as a threshold, rather being linearly related to activity levels (Rydell 1989b). The notable pre-dawn peak for *Myotis*, when nightly temperatures are usually at their coldest, might also be a partial driver for this finding (and may also provide an explanation as to why there was no significant relationship between temperature and activity of soprano pipistrelle; the other species with a pre-dawn peak in activity). Rainfall was negatively correlated with bat activity in all cases (i.e. more registrations in dry conditions). This is consistent with previous findings that rain imposes an additional energetic cost and decreased prey abundance (Erickson and West 2002, Downs and Racey 2007). Wind speed was positively correlated with bat activity in all cases with the exception of *Nyctalus*. This finding is surprising given the potential for additional energetic costs posed by flight in strong winds (Norberg 1990). However, insectivorous bats, and specifically pipistrelles, are known to utilise linear features such as treelines and hedgerows to provide shelter when foraging in windy conditions (Verboom and Spoelstra 1999, Russ et al. 2003). This spatial shift in foraging activity might account for the increase in detected echolocation calls as the detectors used in this study were predominantly placed along linear features as is common in automated surveys (Collins 2016). In this way, automated survey results might be affected by the three-way relationship between the presence of linear features, detector placement and wind conditions.

Moon illumination

Previous studies on the effects of moonlight on bats have shown mixed effects. For example, Lang et al. (2006) found that activity of some insectivorous bats such as the white-throated round-eared bat *Lophostoma silvicolum* in Panama to be lower on moonlit nights, while Appel et al. (2017) found bat activity was positively correlated with moonlight for Parnell's mustached bat *Pteronotus parnellii* and lesser sac-winged bat *Saccopteryx leptura* in Brazil. Here, we found that moon illumination was negatively related to bat activity. This agrees with work by Adam et al. (1994) on the Virginia big-eared bat *Corynorhinus townsendii virginianus* in the US but contrasts with previous work on non-British *Myotis* species,

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which did not find a link between activity and moonlight (Negraeff and Brigham 1995, Hecker and Brigham 1999) – although it is notable that neither of these studies included the modifying effect of cloud cover on illumination.

Although it has been suggested previously that bats at higher latitudes are exempt from the predation pressures that impact tropical species (Karlsson et al. 2002), predation risk on bright nights could still be an important modifier of activity in temperate species (Lima and O'Keefe 2013). It has also been suggested that temperate insectivorous bats may seek more enclosed (shaded) habitats when foraging in bright moonlight (Reith 1982, Erickson and West 2002), such that an apparent decrease in activity in open areas nights might actually be a repositioning of foraging activity spatially. We therefore suggest that the bats in our study might be avoiding bright moonlight conditions because of an increased risk of predation, either real or perceived. Moreover, it is notable that *Myotis* and *Rhinolophus* bats in Europe have previously been found to have an aversion to artificial illumination (Rydell 1992, Stone et al. 2009), which again was provisionally attributed to predation risk.

Implications and recommendations

Bats comprise an important, and legally-protected, part of mammal fauna in the UK. Surveying and monitoring is important in the contexts of scientific research, conservation, assessment of ecosystem health, monitoring progress towards sustainable development goals, and in compliance with legislation on development planning and infrastructure construction (Jones et al. 2009, Barlow et al. 2015, Collins 2016). It is thus vital that the factors which underpin bat activity, and thus detectability in acoustic surveys, are clearly understood. Bat surveys are notoriously difficult to standardise in terms of timing and the abiotic conditions under which they are conducted and only with robust understanding of optimal foraging conditions is it possible for this to be achieved.

We recommend that automated fixed-point surveys are undertaken throughout the night where possible (where this is not possible, they should be conducted for 4 h post-sunset and 2 h pre-sunrise to ensure peak activity times for all species are covered). As long as bats are active, temperature is largely immaterial but nights with heavy rainfall should certainly be avoided. Wind speed should also be taken into account, as linear features might be preferred habitat when shelter is sought from the wind, potentially increasing estimates of activity if detectors are placed close to such features. Surveying during high summer gives the simultaneous advantages of higher activity and greater concentration of activity as nights are shortest. We recommend that given increasing urbanization, the effect of light on bats should be further investigated, and that such research take cognisance of cloud cover as well as lunar phase (Stone et al. 2009, Russo et al. 2017). Given that the findings of this research indicate that overall bat activity decreases when the moon is unobscured by cloud, there remains potential for light from artificial sources to also impact bat activity. Passive monitoring of light levels in the field during surveys might be particularly helpful in such research.

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Supplementary material (available online as Appendix wlb-00659 at <www.wildlifebiology/appendix/wlb-00659>). Appendix 1.

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