

An entrained circadian cycle of peak activity in a population of hibernating bats

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Biological rhythms exist in many diverse forms of life. Individuals must remain entrained to environmental changes to survive. Some hibernating mammals maintain biological rhythms even during deep torpor; however, cues used for entrainment are poorly understood. We studied activity in an assemblage of hibernating *Myotis* bats (mainly *M. nattereri*) inhabiting a temperate maritime climate over 3 consecutive winters using ultrasound detectors and a series of active infrared motion detectors. Here we demonstrate that the timing of peak activity changed as day length changed over winter, but nevertheless remained entrained to a time close to dusk that would be most advantageous for winter foraging. Diurnal activity was infrequent throughout winter. There was an increase in activity at higher hibernaculum temperatures, particularly as temperatures rose above the lower threshold for insect flight (6–10°C). Finally we show that ultrasound detectors and infrared motion detectors produce broadly comparable measures of bat activity within a hibernation site.

Key words: circadian rhythm, hibernation, *Myotis*

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Biological rhythms occur in many species, including animals (Aschoff et al. 1982; Danilevsky et al. 1970), fungi (Bell-Pedersen et al. 1996), plants (McClung 2001), and cyanobacteria (Mitsui et al. 1986). The evolution of biological rhythms in ancient organisms must have generated fitness advantages during the early evolution of life on earth (Hut and Beersma 2011). Fluctuations in the availability of resources occurring at particular times of the day or year may affect behavior and physiology (Hutson 1979). Natural selection will confer a competitive advantage to those individuals that adapt best in terms of energy conservation or the exploitation of resources.

Biological rhythms are driven by both endogenous processes (Hall 1995; Johnson 1926; Moore and Eichler 1972) and entrainment to environmental cues or zeitgebers (Aschoff 1965). Light is considered the foremost of these zeitgebers (Foster and Kreitzman 2004), and in some Arctic species, breeding may be driven by photoperiod alone (Stokkan et al. 2007). However, apparent entrainment to circadian or seasonal cycles in the absence of light (Cavallari et al. 2011) or the light–dark cycle (Pohl 1998) implies that factors such as temperature (Liu et al. 1998) and food (Cavallari et al. 2011; Stephan 2002) are also important zeitgebers.

Both short- and long-term hibernators can maintain circadian rhythms even when using deep torpor (French 1976; Pengelley and Fisher 1961; Twente and Twente 1987), though rhythms

may become attenuated or even eliminated in some species (Heller and Ruby 2004). Arousals may be determined by circadian rhythms that may or may not be associated with specific behaviors such as flight or foraging. Activity and foraging occur during the hibernation season in many insectivorous hibernators (Körtner and Geiser 2000), including some bat species (Ransome 2002). For insectivorous bats the most advantageous time to be active would be shortly after dusk when the risks from predation are reduced, while temperature and, therefore, the availability of insect food remain relatively high when compared with later during the nighttime (Jones and Rydell 1994).

Studies on winter activity in bat populations within hibernation sites using a variety of methods have yielded conflicting results. Daan (1973) used a photoelectric beam splitter and camera, Nagel and Nagel (1997) used a passive infrared light barrier, and Park et al. (1999) used an ultrasound detector and data logger to measure bat activity within hibernation sites. All of these studies showed an increase in activity during nighttime throughout winter.



In contrast, Thomas (1993) used an ultrasound detector and data logger to show that there was little difference in the number of day and nighttime flights within a hibernaculum over winter. Also by using a photoelectric beam splitter and camera, Lubczyk and Nagel (1995) showed an increase in diurnal activity as winter approached. Differences in activity patterns may be due to climatic differences among study sites (Daan 1973) and may also be species specific. There is little adaptive function in synchronizing arousals with dusk (Park et al. 1999) at locations where winter temperatures are below freezing for sustained periods and insect food is therefore scarce.

Some hibernating bat species in North America have experienced rapid population declines in recent years as a result of infection with the fungus *Geomyces destructans*, which causes “white-nose syndrome” (Blehert et al. 2009). Unusual patterns of activity within affected hibernating populations have been observed (Britzke et al. 2010; Reichard and Kunz 2009), leading to dramatic increases in mortality, possibly as a result of premature depletion of energetic reserves (Cryan et al. 2010; Storm and Boyles 2011; Warnecke et al. 2012) or dehydration due to excessive evaporative water loss (Willis et al. 2011). Noninvasive studies on wild bat populations are therefore important in understanding natural activity patterns, and can be used to set a baseline against which aberrant behavior can be detected.

We used ultrasound detectors and a series of infrared motion detectors to measure bat activity close to the entrance of a hibernation site in the south of England over 3 consecutive winters (2007–2010). Because the climate is relatively mild in the United Kingdom and winter foraging opportunities exist (Ransome 2002), we hypothesized that the level of activity recorded would be consistently higher during the nighttime. We also hypothesized that high levels of nocturnal activity would be sustained throughout the winter period, that there would be a shift in the timing of the daily peak in activity with changing photoperiod as winter progressed, and that peak activity would occur at a time similar to when bats emerge from roosts in summer soon after dusk. We predicted that there would be a significant positive correlation between total daily events recorded and tunnel temperature within 1 h of sunset, as bats would have better feeding opportunities on warmer nights. Finally we wanted to better understand if differences in findings shown in other studies could be attributed to the different monitoring techniques used. We therefore tested whether comparable patterns in activity were obtained from results generated by ultrasound detectors and infrared sensors.

MATERIALS AND METHODS

Study site.—Our study site was Greywell Tunnel, a disused canal tunnel on the Basingstoke Canal, Hampshire, southern England, United Kingdom (Ordnance Survey Grid Reference SU 707524). The 1,124-m-long tunnel was constructed in tandem with the canal between 1788 and 1794. The tunnel is approximately 5 m high and has a maximum width of 4.5 m. A

partial collapse during the 1930s (Vine 1994) and a farther fall during the 1950s left the tunnel completely blocked about 800 m from its eastern portal and at 130 m from its western portal for a distance of approximately 190 m. The tunnel is not navigable to boats and grilles (gates) have been positioned at either end to prevent unauthorized human access. These grilles are designed to allow bat access to and from the tunnel. Water depth is approximately 2 m at the eastern end and 2.5 m at the western end of the tunnel, and fluctuates throughout the year by <200 cm at the eastern end and <30 cm at the western end.

Greywell Tunnel has long been known as an important site for hibernating (Stebbing 1993) and swarming (P. Hope, pers. obs.) bats. During hibernation, 5 species of bat in the genus *Myotis* have been recorded using the tunnel. These are Natterer’s bat *M. nattereri*, Daubenton’s bat *M. daubentonii*, whiskered bat *M. mystacinus*, Brandt’s bat *M. brandtii*, and occasionally brown long-eared bat *Plecotus auritus* (though this species was not encountered during our study period). *M. nattereri* often comprise more than 85% of bats counted during hibernation surveys. We conducted a count of hibernating bats during January and February of each year without tactile disturbance.

Frequency-division bat detectors.—Two ultrasound bat detectors (frequency-division) and data loggers (AnaBat II with zero crossing analysis interface module [ZCAIM], Titley Electronics, Brisbane, Australia), each containing a 1-GB compact flash card, were positioned within Greywell Tunnel from the beginning of December until the end of March 2007–2008, 2008–2009, and 2009–2010. Detectors were placed facing into the tunnel at an angle of approximately 45° and a height of approximately 1.5 m from the water’s surface. The detectors were positioned approximately 5 m inside of the grille at both ends of the tunnel. Both detectors were set to continuous monitoring and triggered automatically by ultrasound. We set division ratio to 16 and sensitivity to 4.5 (tests were conducted before the study to achieve the highest sensitivity possible while minimizing background noise) on each detector. To conserve battery power a 3.5-mm din plug was fitted into the microphone socket (to disable the detector speakers) and ZCAIM lights were turned off. Each detector was housed within a protective plastic case that had a hole cut in one end through which the microphone protruded. Detectors were powered via a 12-V 85-Ah recreational battery (life span approximately 35–40 days depending on number of triggered events). Data were downloaded once every 12–14 days and batteries changed every 28–30 days.

Detectors were programmed and data downloaded using dedicated software (CFCRead, version 4.2a and call sequences were analyzed using AnalookW, version 3.3 q software, both available from <http://hoarybat.com>). A bat pass was defined as a file containing a minimum of 2 frequency-modulated sweeps that could be identified as belonging to bats in the genus *Myotis* (Turbill 2008). Due to the difficulty in separating *Myotis* species using frequency-divided recordings of their echolocation calls (Parsons and Jones 2000), bat passes were identified to genus level only. *Myotis* bats are the only species emitting

broadband sweeps in the United Kingdom (Vaughan et al. 1997), and we are confident that all calls recorded belonged to bats in this genus, with the vast majority belonging to *M. nattereri* because of their high relative abundance in the tunnel.

Infrared motion detectors.—We positioned 4 active infrared motion detectors (TrailMaster 1550-PS-BAT, Goodson and Associates, Inc., Lenexa, Kansas) on the grille (so that infrared beams ran parallel to and between selected bars of the grille) at the eastern portal of Greywell Tunnel from the beginning of December until the end of March 2007–2008, 2008–2009, and 2009–2010. Detectors were placed at heights of approximately 0.5 m, 1 m, 1.7 m, and 2.5 m from the water's surface. The active infrared detectors consisted of a transmitter and receiver. An infrared beam traveled between transmitter and receiver and if this was broken for a specified period of time (>45 ms) an event was triggered. The motion detectors that we used were optimized to register bat passes and field trials were conducted before the study to confirm their suitability. Data were downloaded every 12–14 days using a data collector (TrailMaster Data Collector, Goodson and Associates, Inc., Lenexa, Kansas) and then analyzed using a dedicated statistical software package (StatPack, version 2006.123.47, Goodson and Associates, Inc., Lenexa, Kansas). The monitors were each powered by 8 alkaline 1.5-V (C type) batteries with a predicted life span of 6–8 months. Collectively the infrared monitors were able to detect bats passing through approximately 30% of the grille positioned inside the eastern portal of the tunnel. For analysis, data from all 4 motion detectors were pooled.

Measurement of temperature and humidity.—We used 5 temperature and humidity sensors (Tinytag Plus TGP-1500, Gemini Data Loggers Ltd, Chichester, United Kingdom) during winters of 2007–2008, 2008–2009, and 2009–2010. One was positioned at the edge of a canal cutting 100 m outside of the eastern portal; and this was used to monitor ambient temperature. The remaining 4 sensors were positioned within the tunnel, 2 within the eastern end (at entrance and 800 m) and 2 at the western end (at entrance and 130 m). A further 3 data loggers were added in 2009–2010; 2 were positioned within the eastern end of the tunnel (at 100 m and 400 m from the portal) and 1 within the western end (70 m from the tunnel portal). Temperature readings were taken within 1 h of sunset each day and at 6-h intervals thereafter.

All fieldwork followed guidelines set out by the American Society of Mammalogists (Sikes et al. 2011) and where necessary was conducted under license from Natural England (license numbers 20072104, 20082608, and 20092881).

Statistical analysis.—Rayleigh's test for randomness (Zar 2007) was used to assess the distribution of activity recorded by the ultrasound detectors and infrared data loggers over the 24-h period for each study month of each year. To test for correlations between temperature and activity we used Spearman's rank tests as we could not normalize daily activity data from the ultrasound detectors and infrared motion detectors. Spearman rank tests were also used to compare results from the ultrasound detectors and infrared data loggers. We used linear regression to assess how tightly

correlated external temperature and tunnel temperatures were at the eastern (entrance, 100 m, 400 m, and 800 m) and western ends (entrance, 70 m, and 130 m) of the tunnel (tunnel temperature was the dependent variable).

Data were tested for normality (Anderson–Darling test) and nonparametric tests used when appropriate. In comparisons of activity levels between months, we initially conducted a Kruskal–Wallis test and used Bonferroni-corrected Mann–Whitney tests to determine which months differed in median activity. Statistical analyses were conducted using Minitab software release 16.1.1 (Minitab Inc., State College, Pennsylvania).

RESULTS

Over the 3 winter periods 140,973 passes were recorded on the 2 ultrasound detectors, and the active infrared motion detectors registered 26,215 events over the same time period. The ultrasound detector within the eastern end of the tunnel malfunctioned during parts of March 2007 and January 2009, and in the western portal 2 weeks of ultrasound detector data were lost due to equipment malfunction during January 2008. These days, and where necessary months (i.e., monthly totals), have been excluded from analyses. Mean daily temperatures (with *SD* and range in parentheses) between 1 December and 31 March for each winter were as follows: 2007–2008: 6.5 ± 2.9 (–2.4–11.7°C); 2008–2009: 4.2 ± 3.4 (–3.9–10.0°C); 2009–2010: 3.3 ± 3.3 (–4.0–10.3°C).

Daily activity recorded on both ultrasound detectors and on infrared motion detectors differed among months, with activity highest in December (Fig. 1). Hibernation counts (Table 1) show that more bats were counted in the tunnel during January than in February, although differences in activity levels were not apparent between these months. *M. nattereri* comprised $\geq 90\%$ of all bats on 75% of counts.

Temporal distribution of activity.—The infrared monitors showed a very strong nocturnal bias in activity, with the majority of registrations (99%, $n = 26,215$) occurring during the nighttime (Fig. 2b); this pattern of activity remained consistent through the winter period for all study years.

Activity monitored by the bat detector at the eastern portal also showed a strong nighttime bias (85% [$n = 111,497$ passes]) of activity occurred at night; Fig. 2a), although the proportion of daytime activity increased as winter progressed, peaking in February (26%, $n = 32,199$ passes), then decreasing again in March (9%, $n = 20,980$ passes). Daytime activity was not evenly distributed throughout the day but peaked in the time period just before sunset (Fig. 3a).

Activity monitored by the bat detector at the western end also showed a very strong bias toward nocturnal activity (99%, $n = 29,476$ passes). There was a small percent increase in diurnal activity recorded in January (3%, $n = 3,003$ passes) and February (2%, $n = 6,075$ passes) compared with December and March (both $\leq 1\%$, $n = 12,382$ and $n = 8,016$ passes, respectively). A significant nonrandom pattern of activity over

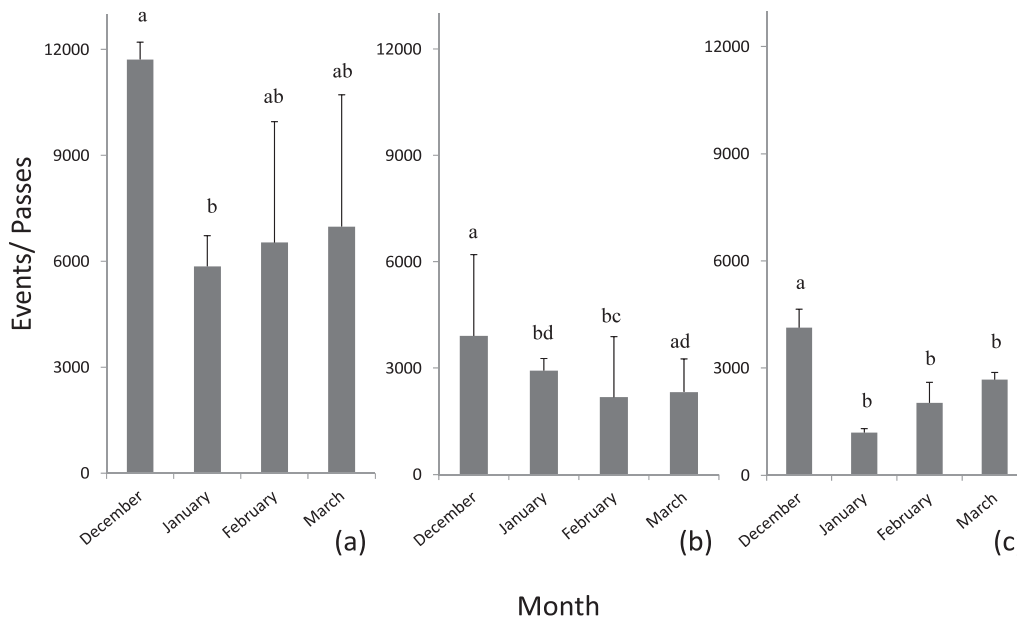


FIG. 1.—Mean monthly activity as recorded by a) ultrasound detector east end, b) ultrasound detector west end, and c) infrared motion detector at the east end of Greywell Tunnel, United Kingdom, with data combined for the winters of 2007–2008, 2008–2009, and 2009–2010. The error bars indicate standard deviations. Months with mean levels of activity that are not significantly different from one another are indicated by the same letter positioned above error bars.

the day was verified using Rayleigh’s tests for each study month during each year (see Supporting Information S1).

A distinct peak in circadian activity was apparent from data recorded by both bat detectors and by infrared monitors. This peak shifted over the winter period, but remained consistent in relation to sunset time as the winter progressed (Fig. 3).

Activity in relation to tunnel temperature.—A significant positive correlation occurred between total daily activity measured on the ultrasound detectors and tunnel temperature measured at the tunnel portals within 1 h of sunset for both east ($n = 322$, $r_s = 0.250$, $P < 0.001$; Fig. 4a) and west ($n = 350$, $r_s = 0.294$, $P < 0.001$; Fig. 4b) ends of the tunnel. A similar relationship was found between tunnel temperature measured at the eastern portal within 1 h of sunset and total daily number of events recorded on the infrared motion detectors ($n = 364$, $r_s = 0.366$, $P < 0.001$; Fig. 4c). Activity increased rapidly once

mean nighttime tunnel temperatures reached $>8^{\circ}\text{C}$ (Fig. 4). We found no correlation between tunnel temperature recorded within the eastern end of the tunnel (at 800 m) and total daily activity recorded on the ultrasound detector ($n = 322$, $r_s = 0.020$, $P = 0.716$) or infrared motion detectors ($n = 364$, $r_s = 0.051$, $P = 0.333$).

Tunnel temperature within the eastern end of the tunnel was positively related to ambient temperature at the tunnel entrance and 100 m into the tunnel, but there was no relationship with ambient temperature and those recorded at 400 m and 800 m from the tunnel entrance (Table 2). Temperatures were very stable at 400 m ($<1^{\circ}\text{C}$ variation, $SD \pm 0.1^{\circ}\text{C}$, $n = 121$) and at 800 m ($SD \pm 0.01^{\circ}\text{C}$, $n = 121$) from the entrance throughout the study period (Fig. 5). However, temperatures within the western end of the tunnel (entrance, 5 m; middle, 65 m; and at a point farthest from the entrance, 130 m) were all influenced

TABLE 1.—Number of bats counted at the east and west ends of Greywell Tunnel, United Kingdom during hibernation survey counts 2008–2010. Numbers of bats counted expressed as a percentage of total bats counted are shown in parentheses.

| Species | 2008 | | 2009 | | 2010 | |
|---------------------------------|------------|-----------|------------|-----------|------------|-----------|
| | January | February | January | February | January | February |
| Greywell Tunnel east end | | | | | | |
| <i>Myotis nattereri</i> | 281 (90) | 14 (88) | 545 (94) | 29 (91) | 263 (93) | 39 (76) |
| <i>Myotis daubentonii</i> | 30 (10) | 2 (12) | 34 (6) | 3 (9) | 20 (7) | 12 (24) |
| <i>Myotis mystacinus</i> | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 311 | 16 | 579 | 32 | 283 | 51 |
| West end | | | | | | |
| <i>M. nattereri</i> | 27 (96) | 8 (89) | 44 (90) | 8 (73) | 35 (90) | 18 (90) |
| <i>M. daubentonii</i> | 1 (4) | 1 (11) | 4 (10) | 3 (27) | 4 (10) | 2 (10) |
| <i>M. mystacinus</i> | 0 | 0 | 1 | 0 | 0 | 0 |
| Total | 28 | 9 | 49 | 11 | 39 | 20 |

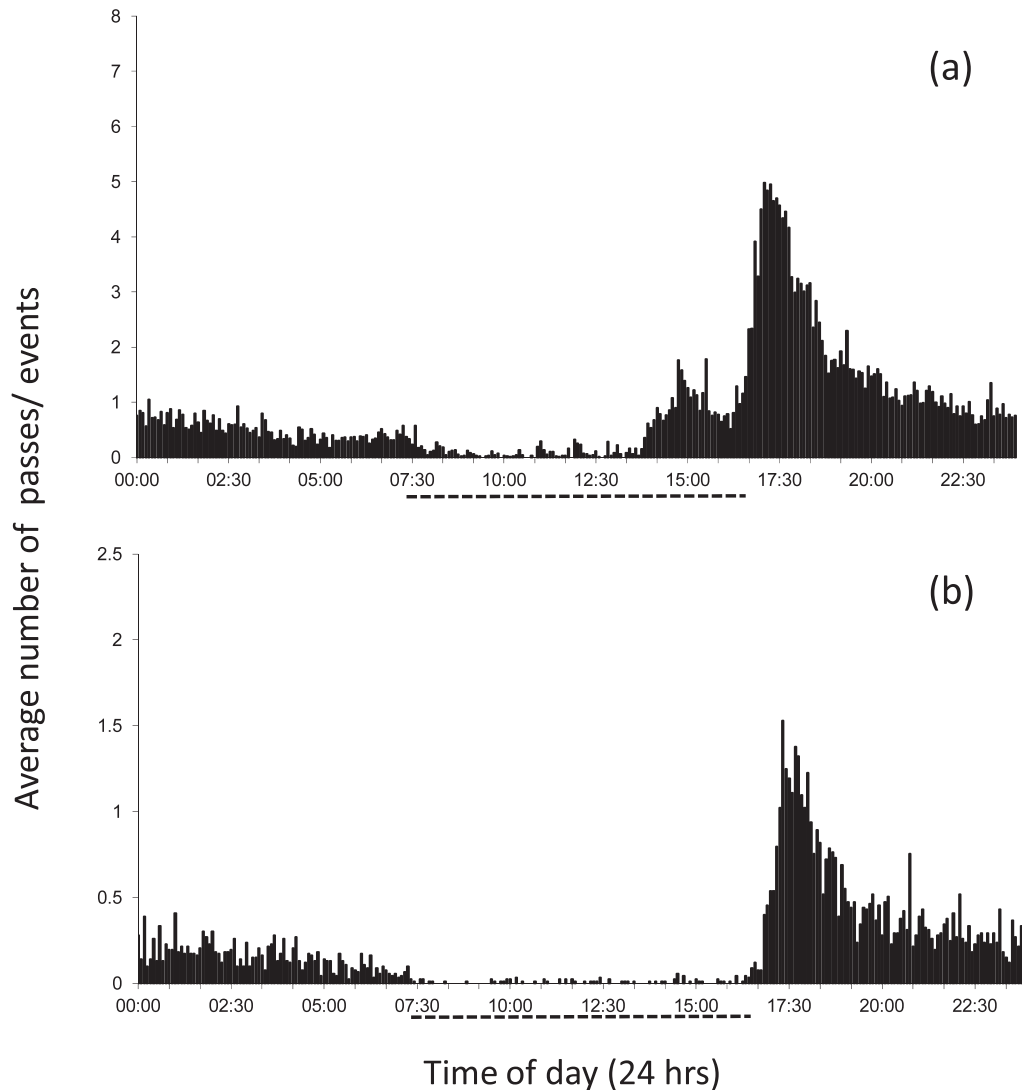


FIG. 2.—Mean activity in relation to time of day recorded at Greywell Tunnel, United Kingdom, over a 24-h day, January 2008, 2009, and 2010 combined. Activity was measured by a) an ultrasound detector (as indicated by passes on y-axis) at the east end of the tunnel and b) infrared motion detectors (as indicated by events on y-axis). Data are binned in 5-min blocks. The dashed line indicates the longest period between sunrise and sunset.

by changes in ambient temperature (Table 2). Nonetheless, changes in ambient temperature once again had less influence on tunnel temperature farther from the entrance.

Finally, there was a significant positive correlation (Spearman rank) between the total daily number of passes/events ($n = 323$, $r_s = 0.445$, $P < 0.01$) recorded by the infrared motion detectors and ultrasound bat detectors.

DISCUSSION

Studies on activity inherently include some degree of pseudoreplication as it is unclear how many individuals are sampled repeatedly across nights. Moreover, a certain amount of autocorrelation will occur with activity data collected on preceding and subsequent nights. We do not believe that pseudoreplication influences the results we report here as the sample size of bats in the hibernaculum was high, and the level

of statistical significance for most tests conducted was high (<0.001 in all cases but one, where it was <0.01).

Our prediction that activity levels would be consistently higher during nighttime was supported. Throughout each month and in all 3 winters of study there was a distinct difference between day and nighttime levels of activity, with consistently higher levels during the nighttime. Our findings are similar to those in other studies (Park et al. 1999; Turbill 2008) conducted at locations with a mild temperate climate, but different from those where bats were studied in continental locations with colder winter temperatures (Lubczyk and Nagel 1995; Thomas 1993), where there was no discernible concentration in the time of activity. The differences in findings among studies indicate that climate may drive differences in activity patterns among study sites.

Ours is the 1st noninvasive study to show a discernible shift in peak activity of a population of hibernating bats that tracks

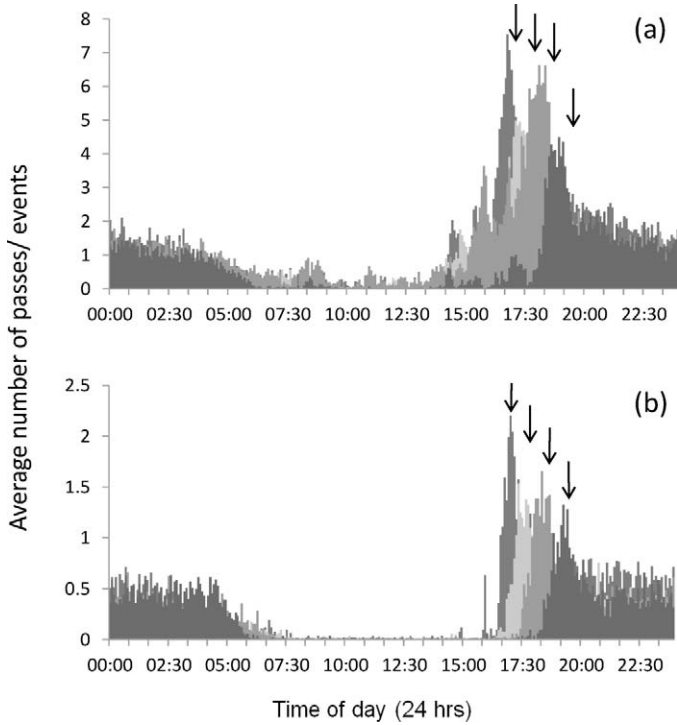


FIG. 3.—Mean number of events each month over a 24-h day at Greywell Tunnel, United Kingdom, December–March 2007–2010 combined. Activity was recorded by a) an ultrasound detector (as indicated by passes on y-axis) at the east end of the tunnel and b) infrared motion detectors (as indicated by events on y-axis) Monthly peaks in activity run from left to right for months December–March. Activity recorded during different months is indicated by different shading patterns. The arrows above indicate the time 75 min after sunset (average for month, December–March), representing the median emergence time of *M. nattereri* during summer.

changing photoperiod as winter progresses. In a study on the greater horseshoe bat (*Rhinolophus ferrumequinum*) Park et al. (2000) demonstrated that arousal time in many individuals was entrained to sunset. A radiotelemetry study on hibernating *M. nattereri* within the western end of Greywell Tunnel (Hope and Jones 2012) performed in tandem with our study demonstrated that individuals aroused frequently (the majority of torpor bouts were <4 days in duration) and that most arousals occurred between 30 min and 1 h after sunset.

Slow-flying or gleaning bat species such as *M. nattereri* emerge from roosts later after sunset than faster-flying species, probably to avoid predation from raptors while still flying when insects are relatively abundant (Jones and Rydell 1994). Insect prey may remain available to gleaning bats at temperatures below the temperature threshold necessary for insect flight. However, prey movements and activity (necessary for gleaning bats to detect prey) are still likely to be highest soon after sunset when temperatures are highest during the night. During the winter nights, warmest temperatures and therefore peaks in insect activity and abundance (Taylor 1963) will occur around dusk. The timing of emergence from winter roosts and therefore entrainment to changes in the time of sunset would be critical so that maximum energetic benefits can be gained to offset any substantial costs of arousal and subsequent flight. Monthly peaks in activity measured in this study corresponded well with known median emergence times recorded (75 min after sunset) from summer roosts for *M. nattereri* within the United Kingdom (Jones and Rydell 1994).

What phase-setting mechanism do bats use in winter to prevent development of a free-running state, so they remain in synchrony with changes in photoperiod? The frequent arousal from torpor observed in bat species that hibernate in regions with mild climates (Hope and Jones 2012; Liu and Karasov 2011; Park et al. 2000; Turbill and Geiser 2008) should help individuals to resynchronize their biological clock to changes in photoperiod. Light is considered the primary zeitgeber for

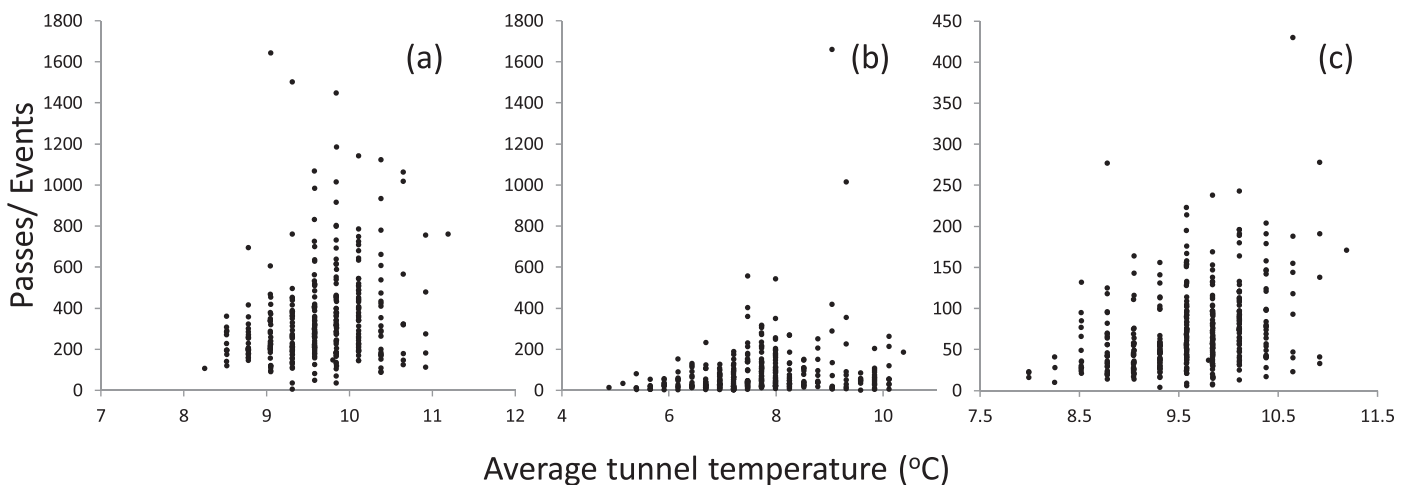


FIG. 4.—Total daily activity in relation to temperature within Greywell Tunnel, United Kingdom during the winters of 2007–2008, 2008–2009, and 2009–2010 combined. Activity was recorded by a) an ultrasound detector situated within the east end of the tunnel (as indicated on y-axis by passes), b) an ultrasound detector situated within the west end of the tunnel, and c) by infrared motion detectors (as indicated by events on y-axis).

TABLE 2.—Results from linear regressions to compare ambient temperature with temperatures at the entrance, middle (100 m and 400 m from east, 70 m from west), and at a point farthest from the entrance (800 m from east, 130 m from west) of Greywell Tunnel, United Kingdom during winter 2009–2010. Temperature data for some analyses were transformed to natural logarithms (\log_e) to achieve normality where appropriate.

| Ambient temperature effect on temperatures within tunnel | Test statistic | | |
|--|----------------|-------|--------|
| | $F_{1,119}$ | r^2 | P |
| East | | | |
| Entrance | 1,764.34 | 93.7 | <0.001 |
| Approximately 100 m | 275.46 | 69.8 | <0.001 |
| Middle, approximately 400 m (\log_e) | 0.16 | 0.1 | 0.689 |
| Farthest, approximately 800 m (\log_e) | 0.35 | 0.3 | 0.553 |
| West | | | |
| Entrance (\log_e) | 154.74 | 56.3 | <0.001 |
| Middle, approximately 70 m (\log_e) | 81.15 | 40.3 | <0.001 |
| Farthest, approximately 130 m (\log_e) | 22.24 | 15.6 | <0.001 |

many organisms, but there is inherent difficulty in sensing changes in the apparent level of light for mammals that hibernate in caves, mines, or tunnels, as light penetration into these sites is usually very poor, especially when mammals are far from entrances.

One behavioral aspect of photoentrainment is light sampling. This behavior has been recorded in rodents (DeCoursey 1986) and is believed to be the chief means of synchronizing biological rhythms to the daylight cycle in bats (DeCoursey and DeCoursey 1964; Voûte et al. 1974). In bats, light sampling usually involves repeated flights within the roost before emergence. Slight differences in results between the ultrasound and infrared detectors may indicate light-sampling

behavior. The higher proportion of daytime activity recorded by the ultrasound detector that was positioned inside of the grille close to the eastern portal can be accounted for by light sampling. Daytime activity was concentrated in the period just before emergence time, indicating that bats were flying up to the grille but not exiting through it until light levels were suitable for emergence.

When tested under laboratory conditions mastiff bats *Molossus molossus* were able to use very low levels of periodic luminance (as low as 10^{-5} lux—the lowest level documented in vertebrates) to maintain photic entrainment (Erkert 2004). Large numbers of hibernating bats often roost close to the eastern entrance (P. Hope, pers. obs.) where variation in both light and temperature would be most pronounced.

Food can also act as a zeitgeber (Stephan 2002) and cavefish retain a food-entrainable clock that oscillates with an infradian rhythm while in complete darkness (Cavallari et al. 2011). For insectivorous bats, however, temperature might be the best indicator of the availability of food. We predicted that there would be higher daily levels of activity at higher tunnel temperatures, and this was indeed the case. Activity levels rose rapidly at tunnel temperatures $>8^\circ\text{C}$; the temperature threshold for flight in many insect species is $6\text{--}10^\circ\text{C}$ (Jones et al. 1995; Taylor 1963). Tunnel temperatures were influenced by changes in ambient temperature but to a lesser degree farther into the tunnel from either portal. This thermal gradient would allow bats to select a roosting place with a more stable temperature should energy conservation be their main consideration (Boyles and Brack 2009; Twente 1955) or a location more influenced by ambient conditions should they need to be aware of potential foraging opportunities.

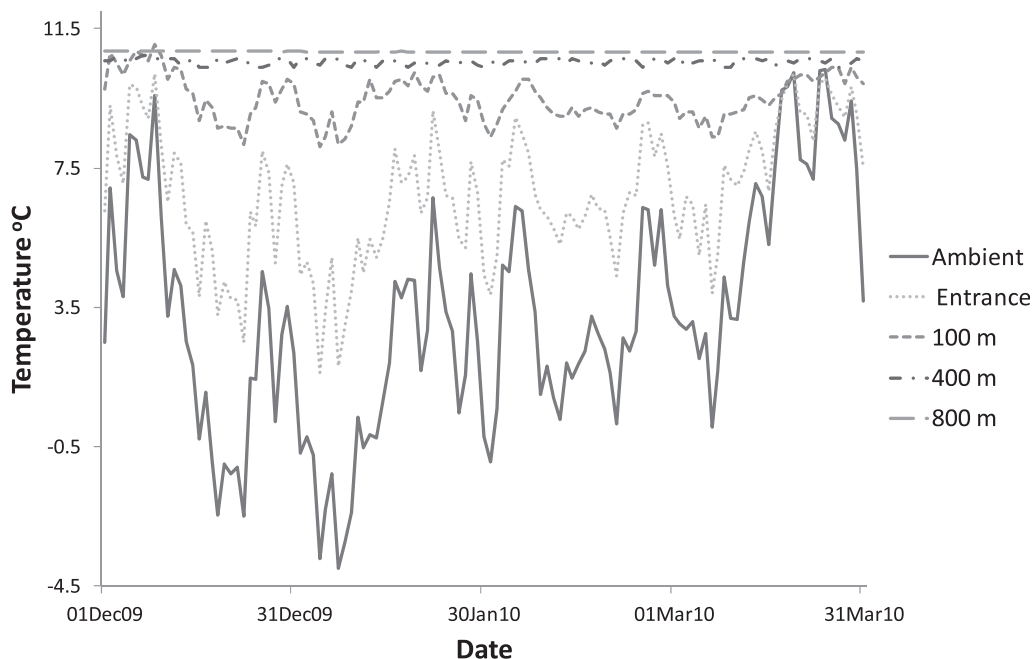


FIG. 5.—Mean daily ambient temperature and mean daily temperature recorded on data loggers within the eastern end of Greywell Tunnel, United Kingdom during the winter of 2009–2010 at the entrance and at 100 m, 400 m, and 800 m from the entrance.

Our final aim was to compare data gathered using the 2 different activity logging techniques. Very similar results in the temporal distribution of activity were obtained using both systems and a statistically significant correlation in total daily events recorded was evident. If entrances are sufficiently small within hibernation sites, active infrared sensors may provide a more accurate measure of bat activity than passive infrared sensors. While using passive infrared sensors in a cave system Nagel and Nagel (1997) found that data loggers were being triggered by other mammalian species and birds. The chance of this happening in our study was much reduced due to the fact that we used an active infrared sensor (the infrared beam that passes between sender and receiver has a limited field of sensitivity and the unit can be situated to reduce false triggers). Also the tunnel has deep water consistently along its entire length, making it difficult for mammals other than bats to enter. Counts of bats were highest in the tunnel in January 2009 and were higher in January than in February in all 3 years. Bats also hibernate in cavities behind the main brick wall of the tunnel (though still fly in the tunnel when active), so our count data may not accurately represent the total number of bats hibernating at the site. Hence further analysis of count data was not considered meaningful.

To maintain a competitive advantage in areas with a mild maritime climate, a hibernating individual must strike a balance between energy conservation and the exploitation of potential foraging opportunities should they arise. Awareness of a rise in ambient temperature to that suitable for increased flight activity of their insect prey and continued entrainment to changing photoperiod, while using bouts of torpor to conserve energy, enables individuals within the population to better exploit these opportunities.

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Rayleigh's test results. Found at DOI: 10.1664/12-MAMM-A-095.1.

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