Seasonal variation in activity by common pipistrelle bats *Pipistrellus pipistrellus* at Durham Cathedral cloister.

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Abstract

1. Observations of activity throughout the yearly cycle by common pipistrelle bats at Durham Cathedral cloister are compared with the results of an intensive study of a hibernaculum and swarming site at Marburg Castle, Germany.

2. The general phenology of activity at Durham is very similar to that at Marburg, with a late summer/early autumn swarming period, late autumn immigration, and evidence of emigration during mild spells from mid-winter onwards.

3. Estimates of numbers of bats visiting the cloister are necessarily speculative, but observations of numbers of grounded bats and of peak numbers of bats flying simultaneously during the swarming period are consistent with an estimate as high as 12000 for swarming and 2600 hibernating.

4. If accurate, such figures indicate that the Cathedral provides a resource for up to 0.5% of the UK population of common pipistrelle, distributed over an area with a 13.8km radius, and may be the largest recorded concentration of the species in the UK.

5. Further investigations are required to test the assumptions on which these estimates of numbers are based, as the site may be of national significance and therefore a candidate for designation as a protected wildlife site.

Introduction

Seasonal swarming by bats during late summer and autumn, in which up to several hundred individuals gather at cave hibernation sites, is associated mainly with the genera *Myotis* and *Plecotus* in the British Isles (Glover and Altringham, 2008), and is thought to be related to mating activity (Parsons et al., 2003). However, similar behaviour also occurs in common pipistrelle, which frequently enters hibernation sites in buildings as well as caves, a phenomenon often referred to as pipistrelle 'invasions' (Sachteleben, 1991, Sachteleben and von Helverson, 2006, Kanuch et al., 2010). Mark-recapture studies indicate that very large numbers may be involved in such invasions over the course of a swarming season, with an estimated 23,000 individual common pipistrelle visiting a hibernaculum in a cellar at Marburg Castle, Germany (Sendor, 2002a).

A common pipistrelle swarming and hibernation site in the 12th Century cloister at Durham Cathedral shares many characteristics with the Marburg site, and is notable for the large number of grounded bats that occur in a typical swarming season. In recent years this has prompted a regular patrol from July to September by members of the Durham Bat Group (DBG), with the purpose of rehabilitating grounded bats. During the 2013 swarming period late opening of the Cathedral during an exhibition of the Lindisfarne Gospels provided an opportunity to monitor the numbers of bats flying in the cloister after sunset, and this was extended into 2014 to provide a picture of year round use of the site. Here I compare the seasonal pattern of occurrence of common pipistrelle at Durham to that recorded at Marburg, and consider whether any evidence can be adduced regarding numbers of bats visiting the cloister during a typical year.

The cloister at Durham Cathedral comprises an outer wall which is square in plan with sides approximately 44m long, comprising the sandstone block walls of the buildings surrounding the cloister, which vary between 8 and 20m in height. An inner wall with empty stone tracery windows surrounds a central lawned garth approximately 34m square. Between the two walls are flag-stoned walkways or ranges, approximately 4m wide and 4m high, and with 15th century wooden beamed ceilings. Above the ceilings are enclosed roof-spaces approximately 0.5m in height where the mono-pitched roof abuts the outer wall. When bats are present they are frequently seen entering and exiting gaps between the ceiling timbers and the stone walling either side, and are assumed to roost and hibernate either within the gaps or in the enclosed roof space.

Method

During the swarming period, and to some extent at other times of year, bats can be observed flying in circuits within the covered walkway surrounding the garth. The overall level of activity was therefore estimated by counting the number of passes with the aid of a heterodyne bat detector. Five minute point counts were performed during the period shortly before and after sunset, during which activity would generally be gradually increasing, if bats were present, due to emergence from roosting sites around the edges of the wooden-beamed ceiling.

During the swarming period, from late July to early October 2013, three point counts were taken separated by two periods of 15 minutes. At other times three consecutive five minute point counts were carried out, often supplemented by several further five minute counts if bats were present. The timing of point counts was varied in relation to sunset to facilitate statistical modelling (see Figure 1). Altogether a total of 300 point counts were performed during 65 visits carried out between June 2013 and June 2014.

Pass frequency was analysed using a generalised linear model with Poisson errors and a log link function, with date and time in relation to sunset as explanatory variables. Date was treated as categorical variable with 65 levels, and time as a continuous variable with a quadratic term.

Results

Bat activity at the cloister generally began somewhat before sunset and continued to build up until around an hour after sunset (see Figure 2). Since point counts taken at different times in relation to sunset are not strictly comparable, assessment of seasonal trends is based on estimates derived from the statistical model of the number of passes at 50 minutes after sunset for each date on which observations were made. This is likely to give the most reliable comparative estimates since it coincides with the modal time period (in relation to sunset) for point counts across the entire year of data recording (see Figure 1).

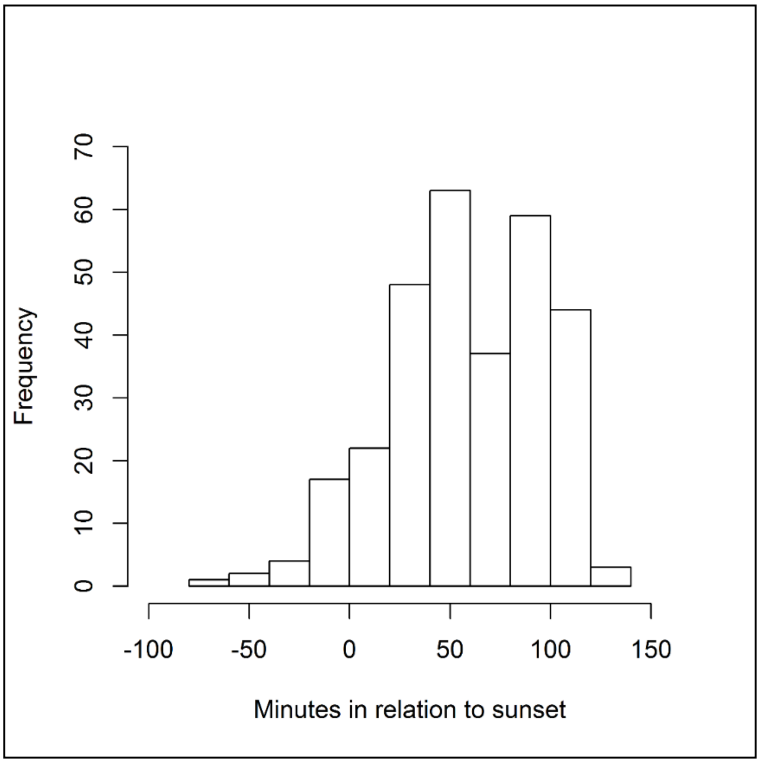

Figure 1 Distribution of five minute point counts in relation to sunset over the entire recording period.

Notable features of the seasonal pattern were the very rapid increase in the numbers of bats in the cloister during July, reaching a peak at the end of the month, followed by a drop in numbers and a second peak at the end of August, then a rapid decline through September (see Figure 3). Bats then appeared to be absent from the cloister until around the time of the first frosts in mid-late November (see Figure 4). Activity from this point onwards was at a very low level compared to the swarming period, but continued intermittently until 11th January. Activity then ceased until 6th February, and again until 19th February, after which intermittent activity continued until 25th March. From this point activity was continuous, either within the cloister ranges or garth, though recording of flight within the ranges was intermittent (see Figure 3).

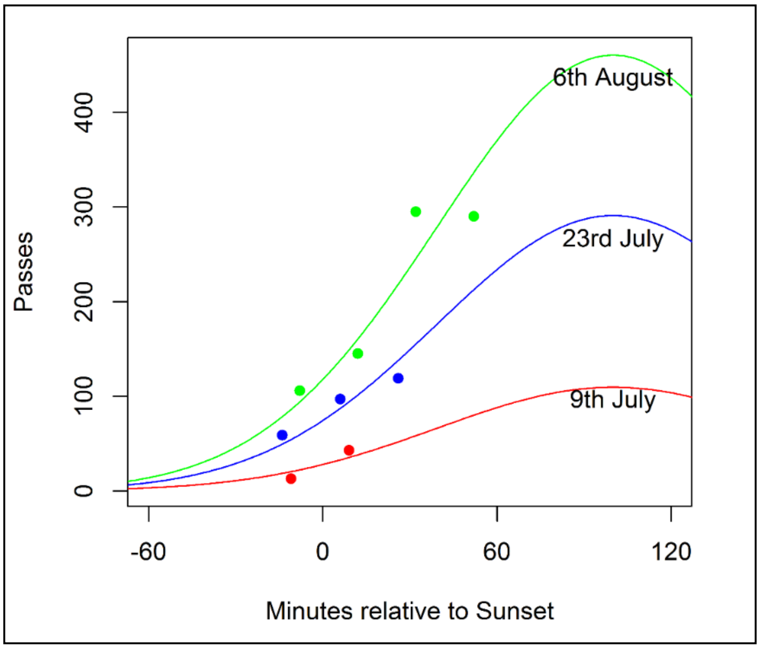

Figure 2 Number of passes per five minute period for three dates during the early part of the 2013 swarming period, along with best-fit lines derived from the GLM.

Bats take approximately 30 seconds to do a circuit of the cloister ranges, and so the number of bats flying at any one time can be estimated from five minute point counts by dividing by 10 (see Figure 4), which indicates that up to 30 bats at least were circling the cloister simultaneously during the peak swarming period. Seasonal variation in this figure can be compared with the number of bats found grounded by DBG over the same period (see Figure 5). Bats were clearly present during mid-June, as several groundings occurred then, but on both observational and grounding evidence they appeared to be absent through late June and early July, reappearing again during the second week of July. Swarming bats then increased rapidly, as assessed by point counts, but this was not reflected by groundings since there was a two week lag before these resumed in the third week of July. Groundings then increased rapidly until the beginning of August and remaining at a relatively high level until the beginning of September, from which both flying and grounded bats decreased rapidly.

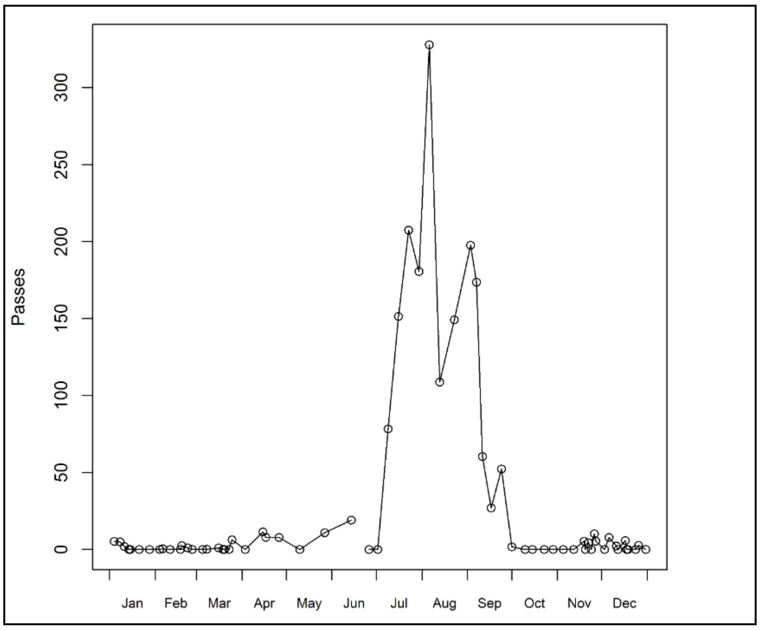

Figure 3 Seasonal variation in estimated number of passes within cloister ranges per five minute period starting 50 minutes after sunset.

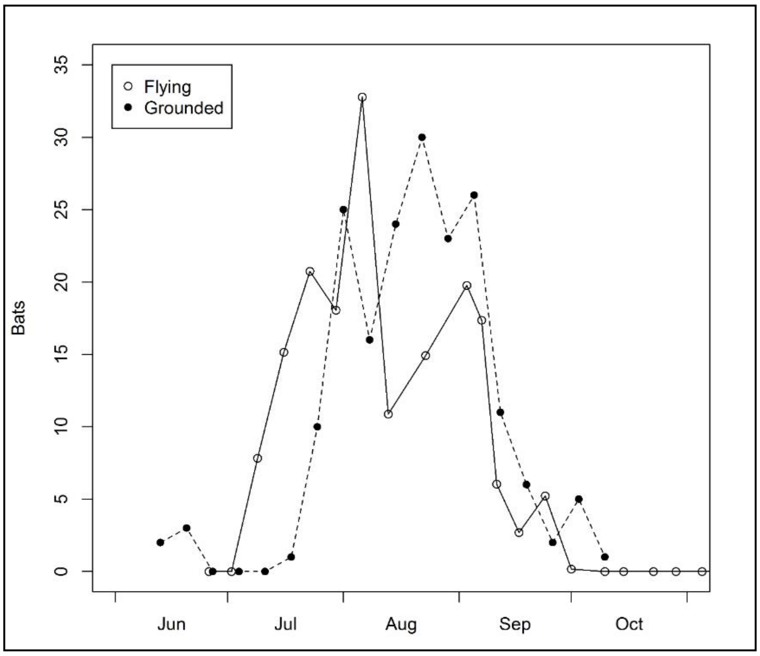

Figure 4 Estimated numbers of bats flying on survey nights, and weekly totals of grounded bats during 2013 swarming period.

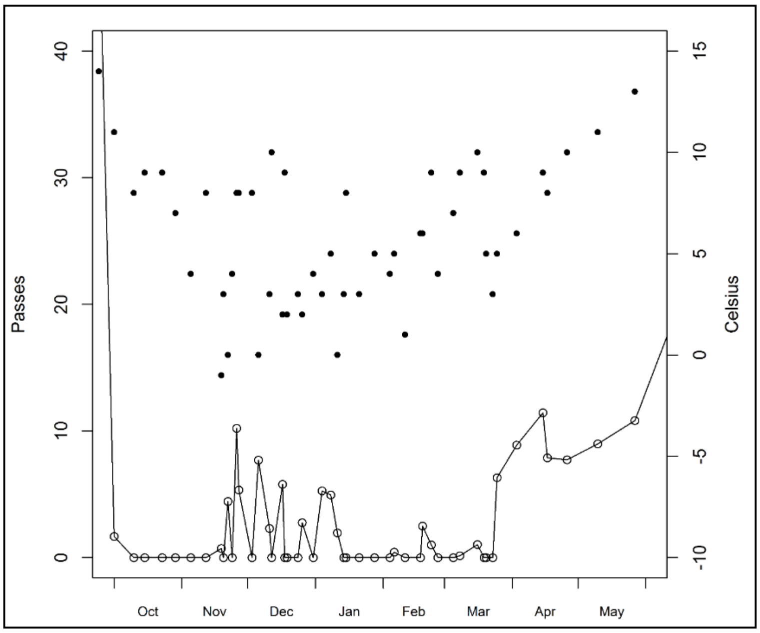

Figure 5 Bat passes per five minute period (open circles) in relation to temperature at 2100 GMT (black dots). Activity from late March includes foraging in the cloister garth.

Discussion

Additional data on bat activity at the Durham Cathedral cloister is available from a consultancy study carried out in 2010-11 (Barrett Environmental 2011 – see appendix A), and the results presented above will be discussed in relation both to this and the study at Marburg.

The purpose of swarming

Sendor (2002b) describes three main theories regarding seasonal swarming by bats: the feeding theory, the mating theory, and the parental guidance theory. The feeding theory explains swarming as concentration of bats responding to local food abundance. Sendor dismisses this as an explanation of the Marburg site where there are few insects available, and this also applies to the Durham Cathedral cloister, since although bats can be seen performing occasional foraging actions within the cloister ranges, the density of insects there is relatively low, and certainly much lower than in the extensive wooded habitat that exists a few tens of metres away in the River Wear gorge at Durham.

The mating theory states that bats gather in swarms in order to mate promiscuously and opportunistically, an idea that is widely accepted for species in the genus *Myotis*. However, Sendor dismisses the possibility that this could explain swarming in *Pipistrellus* species on two main grounds. Firstly, the mating system of *Pipistrellus* species involves resource-based polygyny, with defence of territories by males. Secondly, the late summer/autumn swarming bats at Marburg are mainly females and juveniles. The latter is precisely what is predicted by the parental guidance theory (attributed to Sachteleben 1991), in which swarming reflects maternally-guided visits to potential hibernacula by young of the year, which would otherwise struggle to find suitable hibernation sites.

Sendor relates the difference in swarming behaviour to the relative length of the mating season, which is substantially longer in *Pipistrellus* species due to their shorter hibernation period. Resource-based polygyny therefore maximises fitness in *Pipistrellus* species and comprises an evolutionarily stable mating strategy, whereas in *Myotis* species fitness is maximised during the relatively brief breeding season by promiscuity and opportunistic mating, which is best achieved during autumn gatherings.

The phenology of swarming behaviour

Sendor (2002c) found that the temporal pattern of swarming activity within nights varied according to season. During the summer/autumn swarming period the highest numbers occurred in the middle of the night, following a roughly symmetrical or right skewed pattern of overnight increase and decrease, while a left-skewed pattern occurred during the hibernation period, with most activity immediately after sunset. Observations in the Durham cloister in summer/autumn 2010 indicate a similar pattern, with low numbers immediately after sunset (see Figure A1, Appendix A) and large numbers seen between three and six hours after sunset on 18th August and 7th September (see Figure A2).

The rapid increase in activity seen immediately after sunset at the cloister during the 2013 swarming period almost certainly relates to bats roosting on site, since they could be seen emerging from various points either side of the timber ceiling during the survey. However this also suggests that the increase in numbers later in the night observed in 2010 relates to an influx of bats that have been roosting elsewhere, and this was certainly the case at Marburg as no roosting takes place at the study site during the swarming period. Clearly, therefore, fewer bats were roosting at the cloister during the 2010 swarming season than in 2013, and this raises the question as to whether the numbers roosting reflect the numbers visiting. If so, the mid-night peak of numbers in 2013 may have been even higher than the figures recorded in 2010.

The seasonal pattern of early evening activity supports the idea that this reflects variation in overall numbers, as the pattern of post-sunset variation recorded in 2013 is very similar to the seasonal pattern of numbers visiting Marburg Castle (see Figure 6). Bats present at Marburg during May and early June were exclusively males, and of the five grounded bats at Durham in June 2013 the only two that were sexed were immature males. At Marburg the rapid increase from the beginning of July resulted from an influx of adult females, reaching a peak at the end of July and then beginning to decline around the time that juveniles began to appear. Females then rapidly declined while juvenile numbers continued to increase, resulting in a second peak in overall numbers in late August. At Durham the two-week lag period between the increase in the numbers of swarming bats at the beginning of July, and the beginning of groundings in mid-July, suggests a similar pattern since grounded bats are almost exclusively juvenile. The lag may therefore be explained by the fact that the initial influx involves adult females that are unlikely to become grounded. Additionally, if the increasing trend in numbers of flying bats between mid and late-August is projected backwards, it reaches zero at about the time groundings begin in mid-July, again suggesting that the second peak may be mainly juveniles, and that the mid-August dip reflects an exodus of adult females.

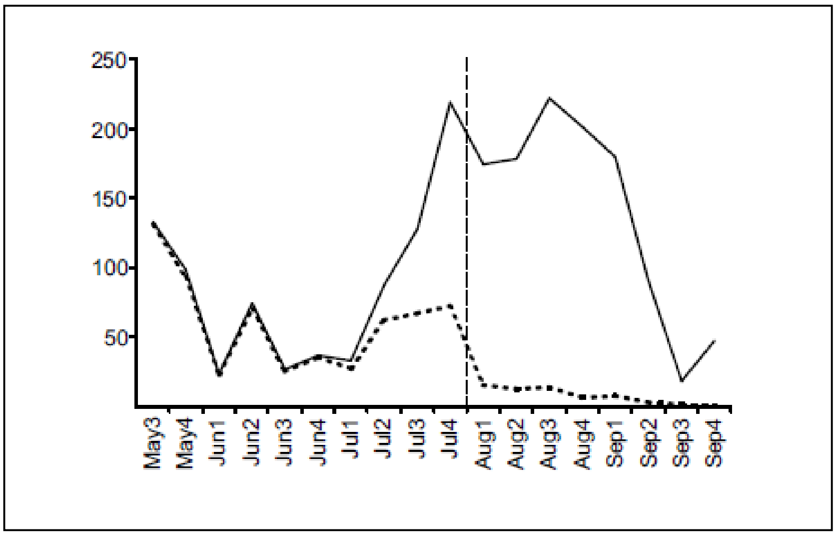

Figure 6 Copy of figure 4.2 in Sendor (2002b). Estimated mean number of bats captured during mist-netting sessions. Solid line represents all bats, dashed line males only, and vertical dashed line the appearance of juveniles at the swarming site.

As at Marburg (Sendor et al., 2000), bats were absent from the cloister for a period of several weeks through October and into November before a resumption of activity coinciding with the first frosts of the year. Habitual foraging by common pipistrelle generally ceases around mid-October at Durham (pers. obs.) after which only small numbers can be detected foraging, even in high quality feeding areas. The majority must therefore enter torpor around this time, despite not appearing in the cloister hibernaculum until late November. Sendor (2002d) recorded a general pattern over several winters of immigration to the hibernaculum during cold weather in the early part of the winter, followed by emigration during mild weather in mid-late winter, and interpreted this as evidence of roost-switching in response to temperature fluctuation. Mass winter hibernacula in common pipistrelle may therefore be frost-free refuges that are used only when cooler hibernation sites are abandoned due to the risk of frost damage.

Sendor attributes such behaviour to an inability of *Pipistrellus* species to accumulate sufficient fat to survive the winter in a thermally stable hibernaculum because of their small size. Instead they resort to colder sites until these become threatened by frost, at which point they transfer to a frost-free location such, putatively, as the Cathedral cloister. The evidence obtained from Durham is consistent with this interpretation. Survey using Anabats placed within the enclosed roof spaces during winter 2010-11 indicated that hibernating bats concentrate in the south-east corner which is presumably the coolest and most thermally stable area on average since it receives the least insolation. Observations in 2013 indicate an influx of bats to the cloister from mid-late November as night-time temperatures drop towards zero (see Figure 4), but the pattern over the rest of the winter is more difficult to interpret, which may be related to the fact that the 2013-14 winter was exceptionally mild.

The winter of 2010-11 was relatively severe, by contrast, and the pattern of activity in relation to variation in temperature was therefore much clearer (see Figure A3). Remote recording by bat detectors positioned within the cloister range indicated some activity during

October, but never exceeding 20 passes over the entire night. This could possibly reflect foraging activity in the garth, but in any case is commensurate with recorded absence on the basis of post-sunset point counts in October 2013. A peak in late November parallels the pattern seen at Durham in 2013, but over the 2010-11 winter both weather conditions and activity patterns diverge from those in 2013-14. Temperatures in 2010-11 were generally between 5 and 10 celsius lower than in 2013-14 (see Figure 5, Figure A3), and there are three striking peaks of activity in January and February 2011 which coincide with the three occasions during that two month period when daily minimum temperature exceeded 5 celsius. These clearly represent emigration events during relatively warm winter periods when the threat of frost recedes, consistent with the view of *Pipistrellus* species hibernation as highly dynamic, with continual transfer between hibernacula throughout the hibernation period.

Interpretation of seasonal activity at Durham Cathedral cloister

On the basis of observations made at Durham in 2010-11 and 2013-14, it is reasonable to conclude that the seasonal pattern of activity by common pipistrelle is essentially the same as that documented by Sendor at Marburg Castle. The relatively low numbers of bats observed in the cloister ranges during spring and early summer are very likely to be males engaged in exploratory investigation of potential hibernacula. From the end of June onwards numbers visiting the cloister build up rapidly as a result of maternally guided juvenile exploration of the hibernaculum, which lasts until the end of September. Apart from occasional foraging in the garth, bats are then absent from the cloister until the first frosts, generally towards the end of November, which prompts immigration to hibernating sites within and above the timber roof beams, particularly above the south range. Numbers then decline from the turn of the year via progressive emigration, which occurs particularly during spells of warmer winter weather.

One of the most striking aspects of bat behaviour at Durham Cathedral cloister is the repeated circling of the ranges by bats, which is particularly evident during the swarming period. This has no obvious function, since the ranges contain few insects and much more profitable foraging locations can be found within a short distance. A clue to the function of this behaviour may come from Sendor's (2002b) observation of a difference in behaviour between adult and juvenile bats affixed with light tags during swarming within the cellar hibernaculum at Marburg. Prior to exiting the cellar via an arrow-slit, adult bats circled several times in front of the point of egress before emerging. Juveniles behaved quite differently however, approaching the exit point 20-25 times and each time flying back into the interior of the 30m long cellar. Sendor remarked that it appeared the juveniles were attempting to assess the dimensions of the cellar, and a similar process might be occurring with the repeated circling of the cloister by bats at Durham, involving a process of familiarization and memory fixing by juvenile bats encountering the hibernaculum for the first time.

Numbers of bats visiting Durham Cathedral cloister

Another aspect of swarming at Durham Cathedral that requires explanation is the large number of groundings that occur each year during the swarming period (see Table 1).

The numbers of bats recovered by DBG are not necessarily comparable across years, due to variation in effort both by the group and independently by Cathedral staff. Caution is also required in assessing totals since repeated groundings of individuals are known to occur. It is certain, however, that up to 90 juvenile bats die in the cloister during the swarming season, the demographic significance of which depends on the number of bats visiting the cloister. At one extreme this may be a catastrophic mortality suffered by a relatively small population, in which case it would be appropriate to search for a causal factor or factors, and at the other it may be simply be an outcome of the normal high level of juvenile mortality in a very large population (see Appendix B).

Year	Deaths	Other grounded	Total
2004	90	64	154
2009	78	95	173
2012	58	126	184
2013	81	157	238
2014	34	49	83

Table 1 Number of grounded bats handled by DBG during the swarming season.

No obvious factor that would cause a high level of mortality to bats is apparent within the cloister. Bats occasionally get trapped within light fittings, but most of the moribund bats that are discovered during the swarming season are simply found on the flooring of the ranges, with a smaller number on the paved area around the edges of the garth. A proportion carry a significant load of external parasites in the form of mites or fleas, but in the majority this is not excessive, and very few show any sign of external injuries, so groundings are unlikely to be caused by collisions with obstacles in the cloister. Furthermore, it would seem unlikely on demographic grounds that this represents a catastrophic mortality to a relatively small population, since its regular occurrence would drive such a population rapidly to extinction, though the possibility remains that the cathedral hosts a 'sink' population that is constantly replenished by immigration.

It is therefore more likely that the groundings are explained by a normal level of juvenile mortality in a large population that visits the cloister during the swarming season, and given the limited information available, a figure of 12,000 bats would appear to be a reasonable, if speculative estimate of the number of individual bats visiting the cloister during the year (see Appendix B). The numbers hibernating at the site will be smaller, since not all bats visiting the site will choose to hibernate there, and at Marburg a population of 5,000 hibernating bats compares to an estimated 23,000 visiting the site. A similar proportion at Durham results in an estimate of 2,600 hibernating bats.

Given these figures it is possible to estimate the catchment area from which the swarming population is derived. Harris et al. (1995) give estimates of up to 0.2 'Pipistrelles' per hectare in areas of suitable habitat. This was prior to the split between common and soprano pipistrelle *Pipistrellus pygmaeus*, so may include some of the latter, but given the high quality of habitat and availability of roost sites in the Durham area it may be reasonable to use this as a basis for an estimate. Thus, if 12,000 bats visit the cloister this represents the population from the surrounding 60,000 hectares, which is the equivalent of a circular area with a radius of 13.8km (see Figure 7). The only other known *Pipistrellus* species swarming sites in the area are Auckland Castle 13km to the south-west, where groundings also occur regularly during the swarming season, though on a much smaller scale, and a site near Piercebridge, west of Darlington (Barrett Environmental 2011).

Significance of the Durham Cathedral swarming and hibernation site

The estimates of numbers of bats are necessarily speculative, but are the best estimate achievable with the limited information available. It should therefore be a working assumption that the cathedral cloister provides a significant resource for 0.5% of the estimated 2.4 million UK common pipistrelle population (Battersby, 2005), spread over an area comprising around half of lowland County Durham. The number using the cloister for hibernation in any one year is likely to be significantly smaller than this, but is also likely to vary considerably with the severity of the winter, with larger numbers resorting to the cloister during winters with significant spells of cold weather. It is a commonplace observation that hibernation sites are the major limiting resource determining the overall density of bat populations, and so the availability of the cathedral cloister may be supporting a significantly higher density of common pipistrelle bats within the catchment area than would otherwise occur. Equally, should any changes occur that render the cloister unsuitable as a hibernation site, the density of common pipistrelle within a wide area around the Cathedral is likely to be significantly reduced.

If the estimates of numbers are of the right order, the population using the cloister will undoubtedly exceed the 1% threshold for the population of the north-east region, so that the site can be regarded as being of at least regional significance for common pipistrelle. However the scale of the annual swarming event at Durham would appear to exceed anything so far recorded elsewhere in the UK, so there is a case to be made that the site should be regarded as nationally significant, and therefore worthy of SSSI designation.

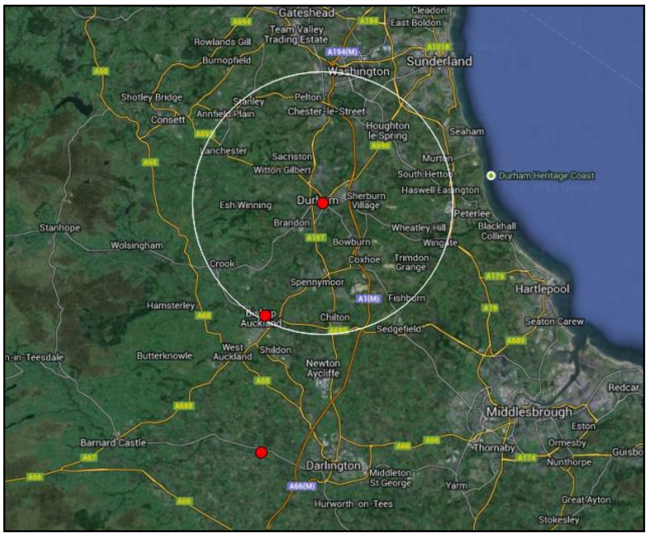

Figure 7 Estimated catchment area for bats visiting the Durham Cathedral cloister, with location of other known swarming sites.

Scope for further studies

Given the potential significance of the site, there is an urgent need to place the estimates of bat numbers using the cloister on a firmer footing. The best solution would involve a mark-recapture survey carried out during the swarming season, but this would be extremely onerous and require a considerable investment of resource. A cheaper and easier alternative might involve vantage point surveys during the swarming period designed to count the number of bats entering and exiting the cloister over the course of a night. If this were practicable it would be possible to test the hypothesis regarding the rapid turnover of swarming bats, and therefore the estimate of the overall numbers involved.

Barrett Environmental (2011) conducted some vantage point surveys using bat detectors around the periphery of the cloister. However most of these were conducted at ground level and appeared unable to pick up incoming bats, since observations of sudden influxes of bats within the garth and cloister ranges were not matched by simultaneous recording of incoming bats by observers outside. This is not surprising given the height of the walls surrounding the cloister, and the limited range within which bat detectors will register bat ultrasound.

A more productive approach may involve bat detector vantage point surveys at the roof level of the buildings around the cloister. Deployment of eight or more observers evenly distributed around the periphery may be sufficient to pick up a high proportion of the bats entering and exiting the cloister. Alternatively, remote recording devices could be deployed at roof level to record bat passes overhead. Such a device or devices could be deployed at a variety of different sites to determine where entry and exit is occurring and would enable continuous recording during the hours of darkness, simplifying the task of estimating the overall number of movements.

It would also be useful to carry out some investigations of the roof void above the cloister ranges to determine exactly how this is used by the bats. A scoping inspection might be performed during October when bats are essentially absent from the cloister. The distribution of bat corpses at this time might indicate the areas used by roosting/hibernating bats, and suggest a protocol for any subsequent inspections intended to estimate numbers when bats are present. In addition it would be useful to record variation in temperature and humidity, particularly over the winter period, to determine whether conditions are indeed relatively stable relative to the exterior, as suggested by the phenology of bat activity.

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Appendix A

Data collected in the Cathedral cloister in 2010-11 (re-analysis from Barrett Environmental 2011).

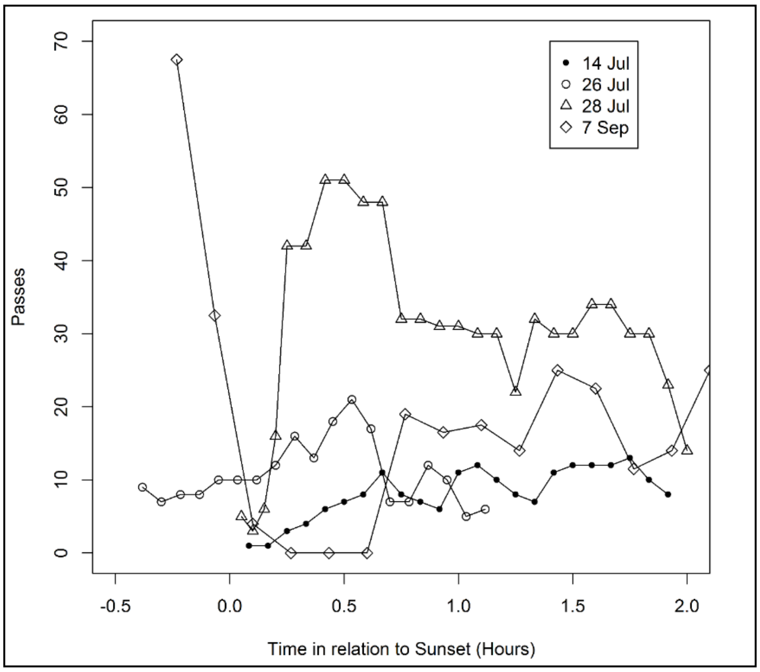

Figure A1 Early-night counts of bat passes in Durham Cathedral cloister per five minute period during the 2010 swarming season.

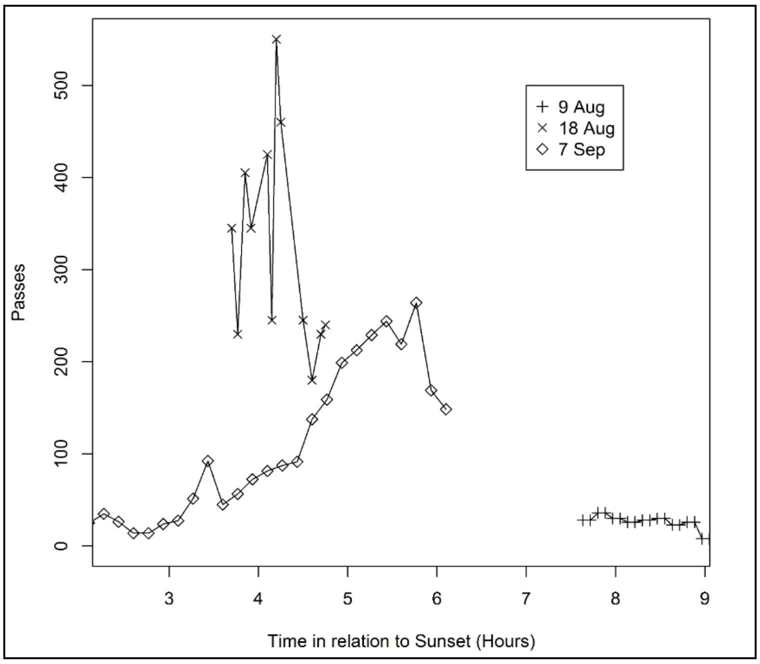

Figure A2 Midnight counts of bat passes in Durham Cathedral cloister per five minute period during the 2010 swarming season.

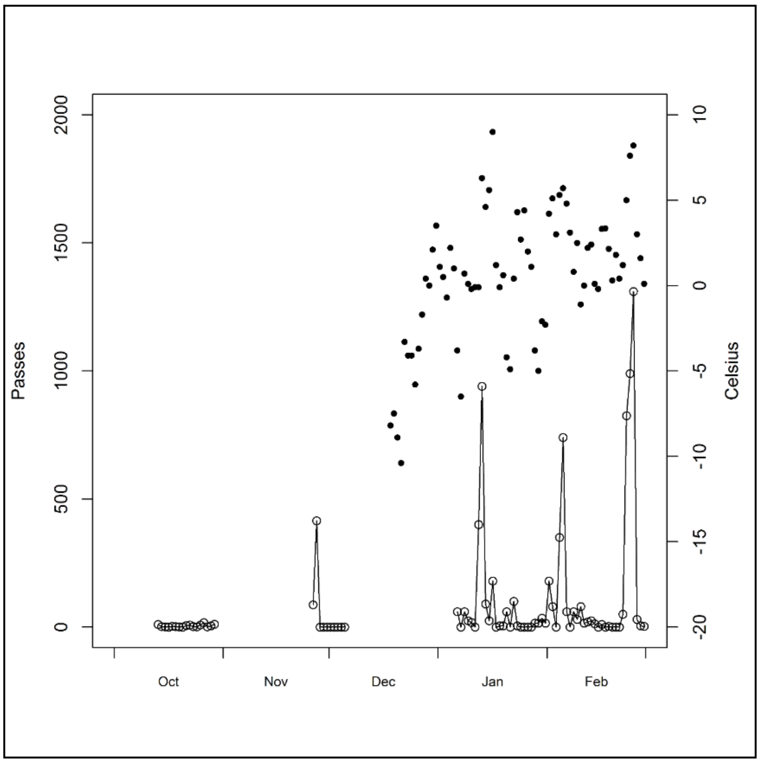

Figure A3 Number of overnight bat passes in Durham Cathedral cloister recorded by Anabat during autumn/winter 2010-11, in relation to daily minimum temperature.

Appendix B

Assessment of numbers of bats visiting the Cathedral cloister during the swarming season

Estimates of the number of bats visiting the cloister can be obtained by two independent methods.

Estimation Method One

It is known that a minimum of 90 juveniles visit the cloister in a good year. Since their mothers also visit, this number can be doubled, and assuming an equal sex ratio and equal likelihood that male bats will swarm/hibernate, it can be tripled, giving a rock-bottom estimate of 270 bats. However this assumes that (i) all juveniles die (ii) all deaths occur in the cloister (iii) all dead juveniles are found. By relaxing these assumptions a more realistic estimate of numbers can be made.

Sendor & Simon (2003) estimate that first year survival in their study population of common pipistrelle is 0.53. Mortality is likely to be 'front-loaded' – i.e. most will occur immediately after the young bats begin to fly or become independent. On the conservative assumption that 50% of young bats die during the swarming period, the estimate of juveniles visiting the cloister can be doubled to 180, and the overall estimate to 540.

However this still assumes that all juveniles die in the cloister and that all are found. If it is assumed that only half die in the cloister, the estimate doubles again to 1080. If only half are found it doubles again to 2160. Even this can be regarded as a conservative figure, particularly if individual bats spend only a short time at the swarming site (see below). If proportions are reduced to one third (deaths, deaths in cloister, discovered deaths) the overall estimate rises to 7290. If it drops to one quarter, the estimate is 12960.

Estimation Method Two

The second method is based on Sendor's (2002b) observation that individual bats spent an average of only 10 minutes at the swarming site. Observations both in 2010-11 and in 2013-14 indicate that 30 is a reasonable estimate of the maximum numbers of bats in the cloister at any one time. Assuming 10 minute visits, if there are 30 bats at time t and no further bats enter, there will be no bats in the cloister at t + 10 minutes, so another 30 bats must enter to maintain equilibrium, i.e. 3 per minute.

Assuming a ten hour night, and on the conservative assumption that the rate of entry increases linearly from 0 to 3 per minute over the first five hours, and decreases from 3 to 0 over the last five, an estimate can be made of the number of bats visiting per night around the seasonal peak.

(i) Over the first five hours bat entry rate accelerates at 3/300 =0.01 per minute, so..
(ii) $dn/dt = 0.01t$, and..
(iii) $n = 0.005t^2$

To get the number of bats that have entered the cloister by the mid-point of the night t is set to 300 (minutes), so $n = 0.005*300^2 = 450$. Since the decline is symmetrical this can be doubled to find the number visiting over the whole night, i.e. 900.

The number for the whole season can be estimated by a similar process. Assuming a 60 day swarming period, if the number visiting per night increases linearly from 0 to 900 over a 30 day period, then declines from 900 to zero for the next 30 days:

(i) Over the first 30 days visit rate accelerates at 900/30 = 30 per day, so..
(ii) $dn/dt = 30t$
(iii) $n = 15t^2$

By mid-season therefore, when $t = 30$, $n = 15*30^2 = 13500$ visits will have occurred, so 27000 visits over the whole season. Sendor's maximum estimate for probability of capture of a marked bat during a trapping session was 0.05, suggesting that the chance of a bat visiting a swarming site in any one night is as high as 1 in 20, i.e. 3 visits per season, which suggests that 27000 visits represent 9000 individuals, the majority of which will be adult females and juveniles. Assuming 4000 of each, this indicates a total of 12,000 bats visiting cloister year round, including spring swarming of males.