Correlates of swarming activity and associated mass mortality among common pipistrelles at Durham Cathedral.

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Abstract

1. Passive monitoring of bat activity within a common pipistrelle *Pipistrellus pipistrellus* swarming site and hibernaculum at Durham Cathedral cloister was carried out between July and December 2017 and post-mortem examination was performed on a sample of bats found dead or dying during the late summer/early autumn 2017 swarming period.
2. High levels of activity were recorded from late July to early October, with a daily peak of activity recorded in the period after sunset, probably reflecting activity of bats emerging from roosting sites within the cloister. The seasonal trend peaked in late August coincident with persistent day flying and a secondary peak occurred in late September.
3. Greater activity was associated with warmer daytime temperatures and lower overnight wind speeds, especially activity in the middle of the night which was also reduced by rainfall in relatively windy conditions.
4. 210 instances of grounding featuring mostly juvenile bats were recorded within the cloister between July and October. Of these, 143 were followed by rehabilitation and release, while the remaining 63 involved bats found dead or which died in captivity. Although grounded bats were generally under-weight, no evidence of disease was discovered in 12 individuals subject to post-mortem examination and while lead concentration was found to be elevated in kidney tissues this was only to sub-clinical levels.
5. Daily frequency of grounded bats was negatively associated with both activity and temperature the previous night, suggesting that groundings are more likely following nights with poor foraging conditions. However, groundings are also positively associated with the volume of contemporaneous daytime activity.
6. The results are consistent with the hypothesis that groundings occur among juvenile bats that suffer energy deficits because their inexperience leads to inefficient foraging. From a demographic perspective this should apply only to a small proportion of juveniles, which would imply that large numbers of bats must visit the site to account for the number grounded.
7. Morbidity related to disease or ingestion of toxins cannot be entirely ruled out, however, since this would require a more intensive regime of post-mortem examination, especially of fresh tissue.
8. Evidence also suggests the possibility that a persistent late September spike in activity within common pipistrelle swarming sites may represent re-immigration to hibernacula prior to entering extended periods of torpor during October. However, contrary to previous findings there was no indication of immigration to the hibernaculum coincident with the advent of sub-zero temperatures late in the year.
9. Further insight into the significance of swarming and associated groundings could be obtained by radio-tracking the movements of rehabilitated individuals, surveying of numbers roosting within the cloister during swarming, use of thermal imaging and long-term continuous passive monitoring of bat activity at the site.

Introduction

Recent research into the significance of swarming behaviour in common pipistrelle has begun to clarify aspects of the species' biology that were previously poorly understood. Hibernation behaviour in particular has been relatively little known, since the species is uncommon at well-studied underground sites (Harris & Yalden, 2008; von Schaik *et al.*, 2015) and the small numbers of hibernating common pipistrelles discovered each winter has failed to reflect their abundance relative to other species (Korsten *et al.*, 2016). However the results of an intensive study of a mass hibernaculum in Germany (Sendor, 2002) have stimulated further investigations, revealing widespread use of mass hibernacula in the urban environment (Korsten *et al*., 2015).

The success of such investigations suggests the generality of Sendor's (2002) findings regarding the relationship between late summer/early autumn swarming and hibernation. The predominance of females and juveniles during the swarming period supports the 'maternal guidance' hypothesis, whereby swarming emerges from visits to prospective hibernation sites by post-breeding females accompanied by offspring of the year, which thereby learn their locations. After swarming dies down towards the end of September, bats are thought to be absent for several weeks before beginning to re-enter hibernacula around the time of the first frosts in late November or December (Racey, 1973). From this point onwards there is a dynamic equilibrium of numbers, with immigration exceeding emigration during cold periods and vice-versa during warm periods until vacation of hibernacula in the spring (Sendor *et al*., 2000; Sendor, 2002 Appendix B).

The generality of these findings is also supported by similar observations made at Durham Cathedral (Bell, 2016), where common pipistrelle swarming and hibernation occur within the cathedral cloister (Figure 1). However this is also the site of mass groundings and mortality of bats during the swarming period for which there is no obvious cause, although Bell (2016) speculated that it might simply reflect a normal level of post-fledging mortality if the numbers visiting the cloister are sufficiently large. If so, the site may be highly significant for regional populations of common pipistrelles, but if smaller numbers are present the mortality may be regarded as unusual and requiring explanation.

Either way, the situation demands further investigation and Durham Bat Group (DBG) has therefore resolved to initiate a long-term study of the year-round use of the Durham Cathedral cloister by common pipistrelles. From July 2017 continuous monitoring of bat activity in the cloister has been carried out using a remote logger and during the 2017 swarming period a number of the casualties recovered from the cloister by DBG volunteers were sent for autopsy to investigate possible causes of mortality. The results of the latter and an analysis of monitoring data up to December 2017 are presented here.

Figure 1: View from south east corner of Durham Cathedral cloister towards the western towers.

Method

Monitoring of bat activity

Continuous (24-hour) monitoring of bat activity was carried out using an Anabat Roost Logger installed within the cloister. This records ultrasound in zero-crossing format using a microphone with a sensitivity peak at 42Khz. Sounds resembling bat calls are then extracted in the form of files suitable for analysis by Analook software. A single bat-like call generates a file containing all sounds recorded during a minimum period of five seconds (by default) starting immediately before the call. If additional bat-like calls are recorded within this period it is extended for a further five seconds up to a maximum of 15 seconds. Each file can therefore contain anything between a single bat call and multiple complete bat passes.

The number of files generated in each hourly period was used as an index of bat activity, which if continuous would generate an index of 240 (one hour = 240 x 15 seconds), while a single bat call every five seconds would generate an index of 720 (one hour = 720 x 5 seconds). Either estimate may therefore represent the presence of anything from a single bat to several hundred, so the index provides only a crude measure of bat activity and the number of bats present. However, the swarming behaviour at the cloister has long been observed to involve repeated circuits of the cloister ranges (Bell, 2016), in the context of which the frequency of sound file generation by a passive logger may provide an economical method of indexing activity over a long period.

Data analysis was performed using R version 3.1.2. (R Core Team, 2014), with plots generated using the 'Akima' and 'plot3D' packages. Analyses of bat activity and frequency of bat groundings were performed in all instances using quasipoisson errors and a log link function. Data for local variation in sunrise and sunset and of weather variables were obtained from www.timeanddate.com.

Cloister inspections

The cloister was searched on a near-daily basis for grounded bats between late July and mid-October. Because the searches were carried out by several volunteers on a rota basis, they were not performed in a systematic fashion. Timing of searches varied, as did the degree of liaison with various cathedral staff who recovered grounded bats for collection by bat group volunteers. Numbers of bats recovered on a particular date cannot therefore be regarded as an exact or consistent measure of the number of bats grounded on that date, but may reflect daily variation to an extent that rewards analysis in relation to potential causal variables

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Post-mortems

Grounded bats that were discovered alive during cloister searches were taken into captivity for rehabilitation and release. However, a proportion of the bats found had already died prior to discovery and some of those recovered alive subsequently died in captivity. A sample of these casualties was prepared and transported to APHA laboratories in Exeter for post mortem examination. Corpses were preserved in 10% neutral buffered formalin solution immediately after discovery or the death of a captive bat, with a dorsal incision made to ensure fixation of the internal organs prior to sectioning for histological staining.

Results

Diurnal and seasonal variation in activity

Bat activity within the cloister was recorded continuously from 19/07-31/12/2017 and the results are illustrated in Figure 2.

Substantial activity occurred from the beginning of this period until early October, with a marked peak closely following sunset both in the sense of daily chronology and seasonal variation. Sunset varied between 21:29BST on 19/07/2017 and 18:41BST on 01/10/2017 and throughout this period maximal activity followed within one to two hours. This produced a peak daily activity index exceeding 100 per hour for much of the period, with activity continuing at over 50 per hour for about five hours after sunset before gradually declining towards sunrise. When peak activity exceeded 150, activity levels in excess of 50 per hour continued almost until sunrise.

Substantial day-time flying occurred during August and September and in the second half of August some bat activity occurred throughout most of the day, with the exception of the three to five hour period before mid-day. Activity declined rapidly from the beginning of October and did not exceed a handful of recorded bat passes per night during November and December, with no recorded activity on the majority of nights.

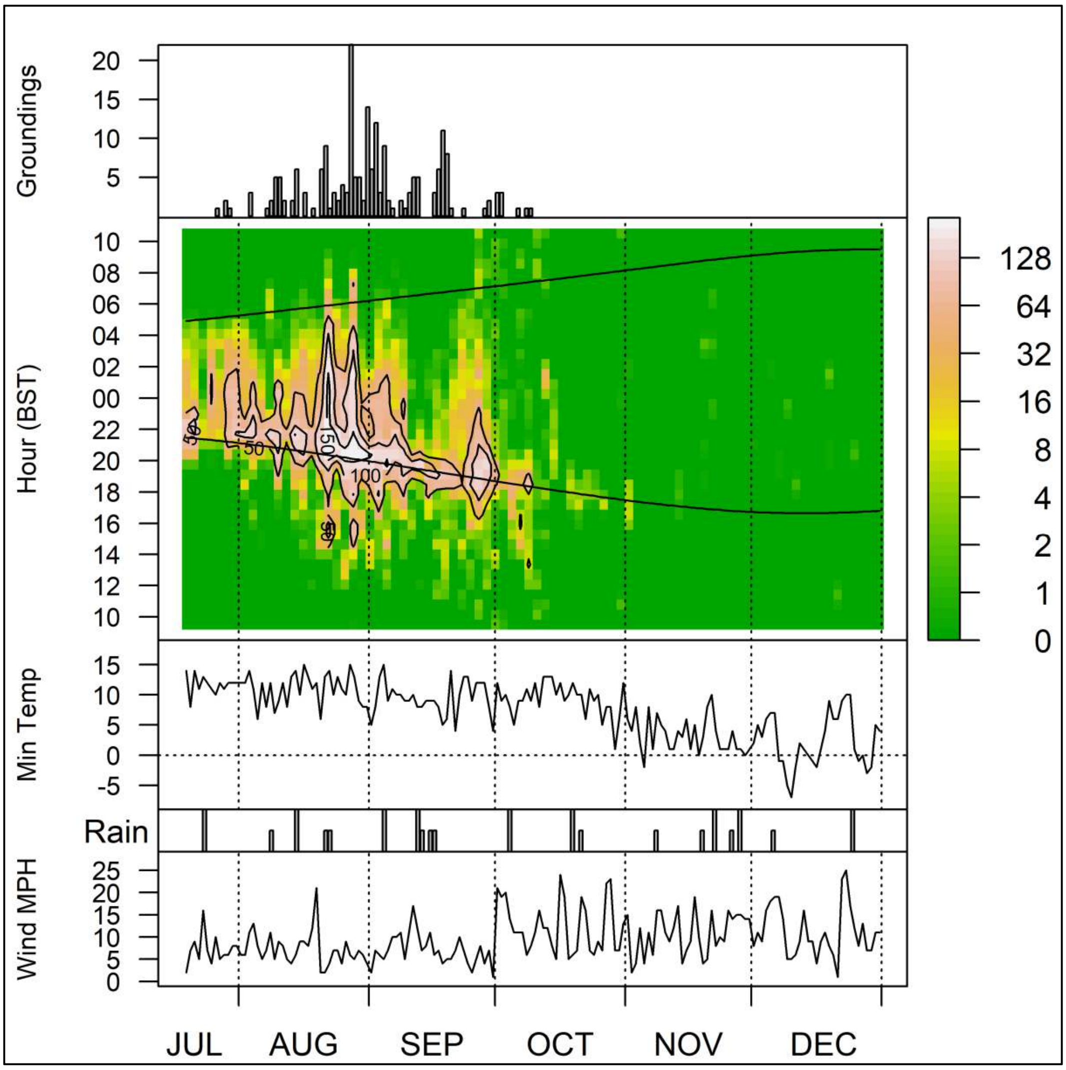

Figure 2: Topographic plot of bat activity at Durham Cathedral cloister in relation to weather conditions and number of grounded bats per day. Contours show the index of bat activity (sound files generated per hour) on a linear scale and colours on a geometric scale to disclose low levels of activity. Curved lines indicate the seasonal trend in sunrise and sunset. All diurnal indices are shown in relation to British Summer Time (GMT+1). The rain chart indicates the occurrence of overnight rainfall either before or after midnight only (short bar) or both before and after midnight (tall bar). The temperature plot shows overnight minima, and the wind plot shows the higher of the average wind speeds recorded between 1800-2400 and 0000-0600 hours.

Correlates of activity

Daily patterns of variation in bat activity indices at the cloister suggest that these may be usefully broken down into successive stages with varying behavioural and functional significance. Correlates of variation in cumulative diurnal activity during the main swarming period between 25/07-31/10/2017 inclusive (81 days), were therefore analysed separately for (i) Daytime: i.e. the period between sunrise and sunset, (ii) Post-sunset, i.e. the two hour period after sunset when peak activity occurs, and (iii) Mid-night, i.e. the period between two hours after sunset and sunrise (Table 1). In each case the candidate explanatory variables included a cubic function of date to account for any underlying trend, a three-way interaction of daily maximum temperature, overnight wind speed and rainfall and a count of the number of rehabilitated bats released each day at the cathedral.

The results for all three indices demonstrate a positive effect of daily maximum temperature, which proved more predictive than both temperature at sunset and the previous night's minimum and a negative effect of wind in addition to an underlying quadratic trend. However the variables proved to have the greatest explanatory power in relation to activity during the mid-night period, for which the negative effect of wind speed showed a significant interaction with rainfall. Data for dates with overnight rain were relatively scarce (Figure 2) but suggest that mid-night activity declined more gradually with increased average wind speed on dry nights than on nights with rain (Figure 3).

The sums of fitted values for the models of daytime, post-sunset and mid-night activity account for 77% of the deviance in cumulative daily activity (null deviance = 25109, residual deviance = 5696) and explains much of the wide variation in activity levels from day to day, apart from exceptionally high levels that occurred from late September onwards (Figure 4).

Table 1: Analysis of deviance in activity indices in relation to date, weather and numbers of rehabilitated bats released, performed via backward deletion of non-significant variables. Temperature refers to same-day maximum and wind and rain to the previous night (Figure 2).

	Daytime		Post-sunset		Mid-night	
Null deviance	11323 (80df)		5692 (80df)		17537 (80df)	
Residual deviance	4766 (76df)		2304 (76df)		5178 (74df)	
	Effect (SE)	P	Effect (SE)	P	Effect (SE)	P
Date	**0.1336 (0.0223)**	**<0.0000*** **	**0.0544 (0.0100)**	**<0.0000*** **	**0.0499 (0.0163)**	**0.0030** **
$Date^2$	**-0.0013 (0.0002)**	**<0.0000*** **	**-0.0007 (0.0001)**	**<0.0000*** **	**-0.0007 (0.0002)**	**0.0028** **
$Date^3$	0.00001 (0.00001)	0.4010	-0.000003 (0.000007)	0.6256	-0.00001 (0.00001)	0.3222
Temperature	**0.2598 (0.0506)**	**<0.0000*** **	**0.1200 (0.0320)**	**0.0003*** **	**0.3321 (0.0535)**	**<0.0000*** **
Wind	**-0.0504 (0.0232)**	**0.0330* **	**-0.0380 (0.0146)**	**0.0113* **	**-0.0690 (0.0282)**	**0.0169* **
Rain	-0.0370 (0.1494)	0.8048	0.0406 (0.0945)	0.6686	**1.0566 (0.4603)**	**0.0245* **
Released	0.0325 (0.0182)	0.0780	-0.0074 (0.0161)	0.6490	0.0086 (0.0233)	0.7122
Temperature x Wind	-0.0225 (0.0117)	0.0582	0.0022 (0.0091)	0.8119	-0.0158 (0.0161)	0.3297
Temperature x Rain	0.0076 (0.1219)	0.9506	0.0645 (0.0788)	0.4159	0.2314 (0.2245)	0.3060
Wind x Rain	0.0510 (0.0397)	0.2032	0.0229 (0.0285)	0.4251	**-0.2049 (0.0889)**	**0.0241* **
Wind x Temperature x Rain	-0.0187 (-0.0239)	0.4359	-0.0116 (0.0181)	0.5252	-0.0288 (0.0609)	0.6382

Grounded bats

Cloister inspections were performed on 57 days during the 81 day period between 25/07-31/10/2017, with only seven days missed during the 51 day period of the highest activity between 07/08-25/09/2017. In total 210 groundings were recorded, of which 143 resulted in rehabilitation and release and 67 featured bats found dead or which subsequently died. Released bats were not marked, so repeat groundings may account for a proportion of the total. Only 201 of the groundings were assigned to their date of discovery for subsequent analysis as nine of the bats found dead were either mummified or partially decomposed and had therefore clearly been dead for some time.

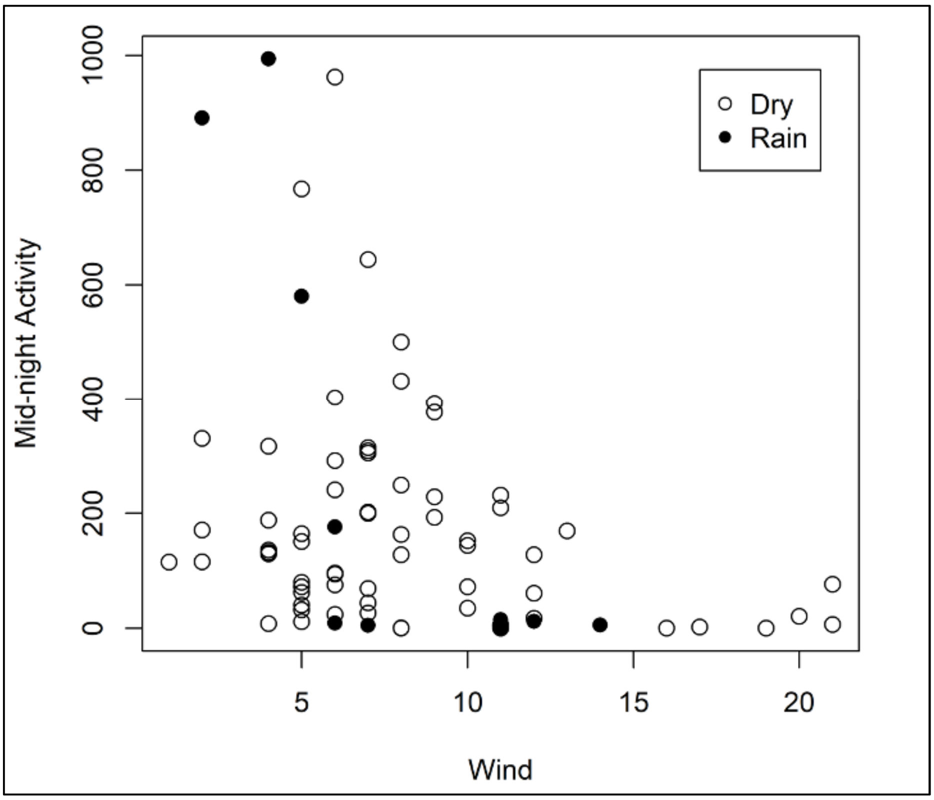

Figure 3: Activity indices during mid-night period in relation to wind speed and rainfall.

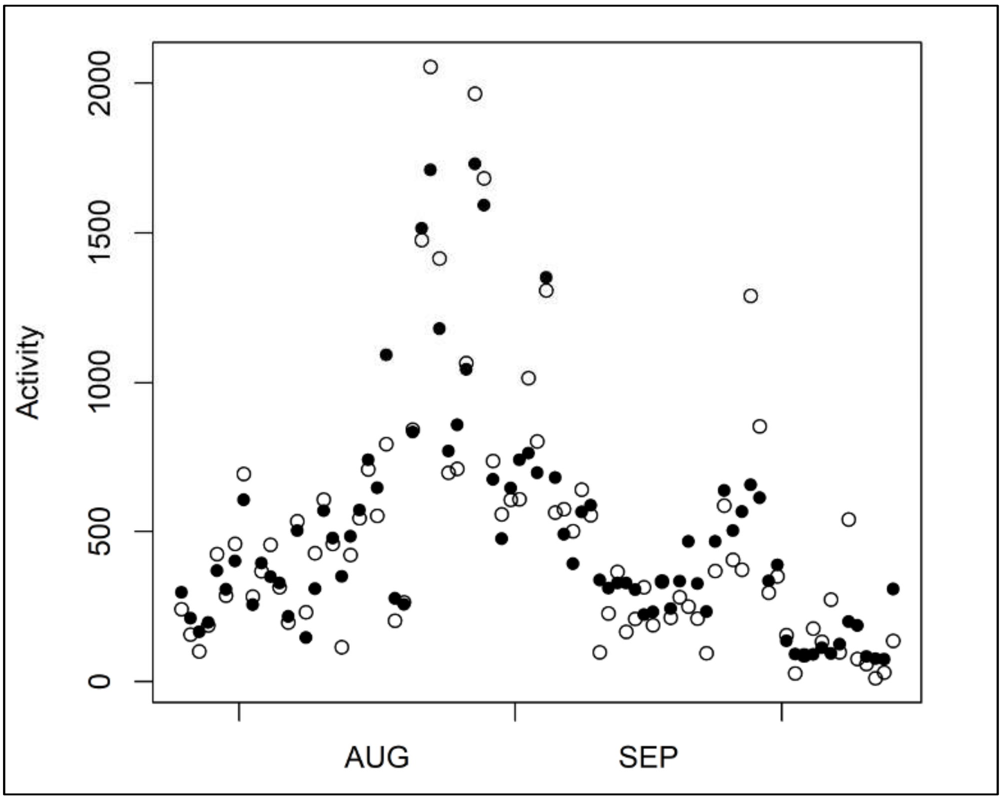

Figure 4: Sums of fitted values for models of daytime, post-sunset and mid-night activity (dots) versus observed cumulative daily activity (circles).

A marked peak in the number of groundings occurred towards the end of August, although as with activity there was much variation in numbers from day to day. The 22 bats recovered on 27/08/2017 far exceeded the next highest daily frequency (14 on 31/08/2017), but only three and five bats were recovered on the preceding and following days, respectively.

Sex, age and weight
Not all the bats located were sexed and aged, but among those that were the sex ratio was even and the vast majority were identified as juveniles (Table 2).

Table 2: Contingency table of sex and age among grounded bats.

	Male	Female	Not sexed	Total
Adult	3	2	0	5
Juvenile	36	35	8	79
Total	39	37	8	84

Weights at discovery of a sample of the bats obtained from the cloister in 2017 are compared in Figure 5 with a sample of juvenile common pipistrelles and soprano pipistrelles *P. pygmaeus* obtained from nearby Hamsterley Forest in August and September 2016, from which it can be seen that the cathedral bats are clearly underweight.

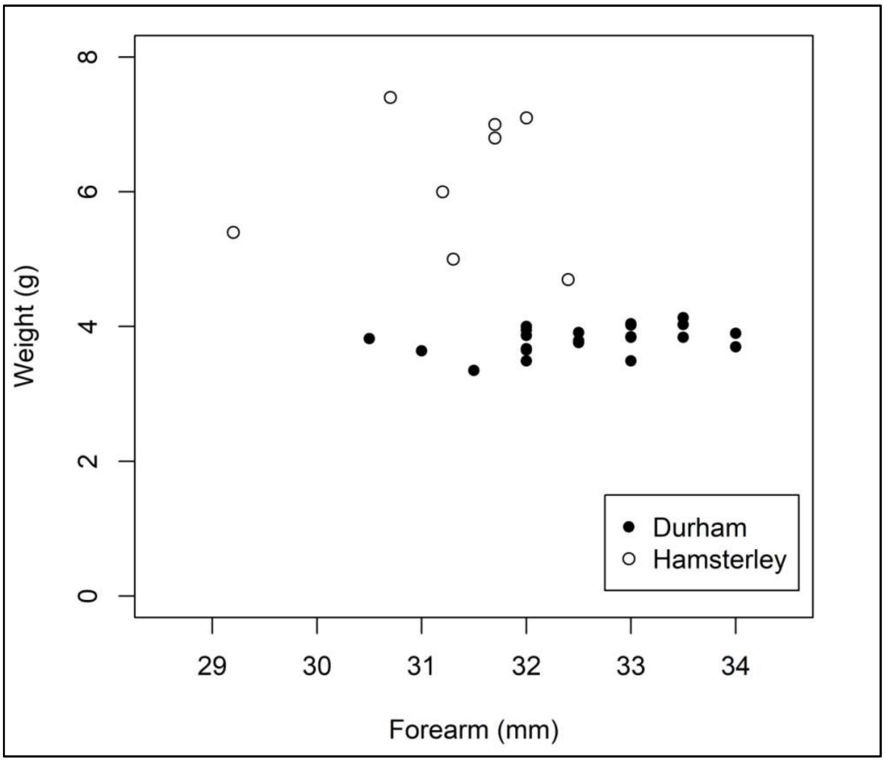

Figure 5: Plot of weight against forearm length of grounded common pipistrelle bats from Durham Cathedral in August/September 2017 and juvenile common and soprano pipistrelles from bat boxes at Hamsterley Forest, County Durham in August/September 2016.

Correlates of grounding frequency
The number of bats located within the cloister on a particular date may have been affected by the fact that cloister inspections were not systematic. Inspections could take place in the morning or afternoon/evening when bats could sometimes be observed becoming grounded immediately after emerging from roost sites at the edges of the wooden beamed range ceilings (Figure 6).

Morning inspections would therefore be likely to miss such groundings, which would not be discovered until the following day. Likewise the numbers on a particular day might include groundings from previous days whenever a gap in inspections occurred. A two-level categorical variable was therefore defined with a value for a given date that varied according to whether inspections occurred before or after midday and an additional three-level variable was defined according to whether inspections had occurred on the previous day either before midday, after midday or not at all. However, neither variable was found to significantly affect the number of groundings recorded (inspections on same day: Δdeviance = 4.6151, $F_{1,51}$ = 2.3682, P = 0.1300; inspections on previous day: Δdeviance = 5.4318, $F_{2,47}$ = 1.4543, P = 0.2439).

Figure 6: North range of the cloister looking east towards the south transept.

Variation in the daily frequency of grounded bats was analysed in relation to a cubic function of date, activity indices for daytime and post-sunset and mid-night periods and the interaction of temperature, wind and rainfall. In addition to an underlying convex quadratic trend, significant deviance was explained by mid-night and daytime activity, but in opposite directions, with a positive effect on frequency of groundings of daytime activity and a negative effect of activity during the previous mid-night period (Table 3a). The model explained half of the null deviance, again including considerable day to day variation, but failed to account for the very high numbers on 27/08/2017, or the flurry of high frequency days in mid-September (Figure 7). No direct effect of weather conditions was detectable independent of activity indices, but when the latter were excluded a significant decline in number of groundings with increased overnight minimum temperature was detectable (Table 3b).

Table 3: Analysis of deviance of daily grounded bat numbers. Wind, rainfall, overnight minimum temperature and mid-night activity indices are for the preceding night, and daytime and post-sunset activity indices for the daytime period to which the count of grounded bats refers. Backward deletion is performed a) with and b) without activity indices.

	Null deviance = 208.98 (56df)			
	a) Residual deviance = 104.00 (52df)		b) Residual deviance = 135.14 (53df)	
	Effect (SE)	P	Effect (SE)	P
Date	**0.0819 (0.0290)**	**0.0067****	**0.1090 (0.0328)**	**0.0016****
$Date^2$	**-0.0012 (0.0003)**	**0.0016****	**-0.0015 (0.0004)**	**0.0005*****
$Date^3$	-0.000009 (0.00002)	0.6371	-0.000006 (0.00002)	0.8371
Temp	-0.0500 (0.0432)	0.2524	**-0.1048 (0.0438)**	**0.0202***
Wind	0.0021 (0.0306)	0.9451	0.0227 (0.0304)	0.4580
Rain	0.0008 (0.3201)	0.9981	-0.0118 (0.3203)	0.9707
Daytime	**0.0030 (0.0007)**	**<0.0000*****		
Post-sunset	0.0025 (0.0026)	0.2298		
Mid-night	**-0.0019 (0.0007)**	**0.0006*****		
Temp x Wind	0.0009 (0.0121)	0.9421	0.0128 (0.0126)	0.3168
Temp x Rain	-0.0072 (0.1560)	0.9635	-0.0766 (0.1302)	0.5589
Wind x Rain	0.0756 (0.1039)	0.4706	0.0020 (0.1235)	0.9869
Wind x Temp x Rain	0.0520 (0.0747)	0.4905	0.0285 (0.0796)	0.7224

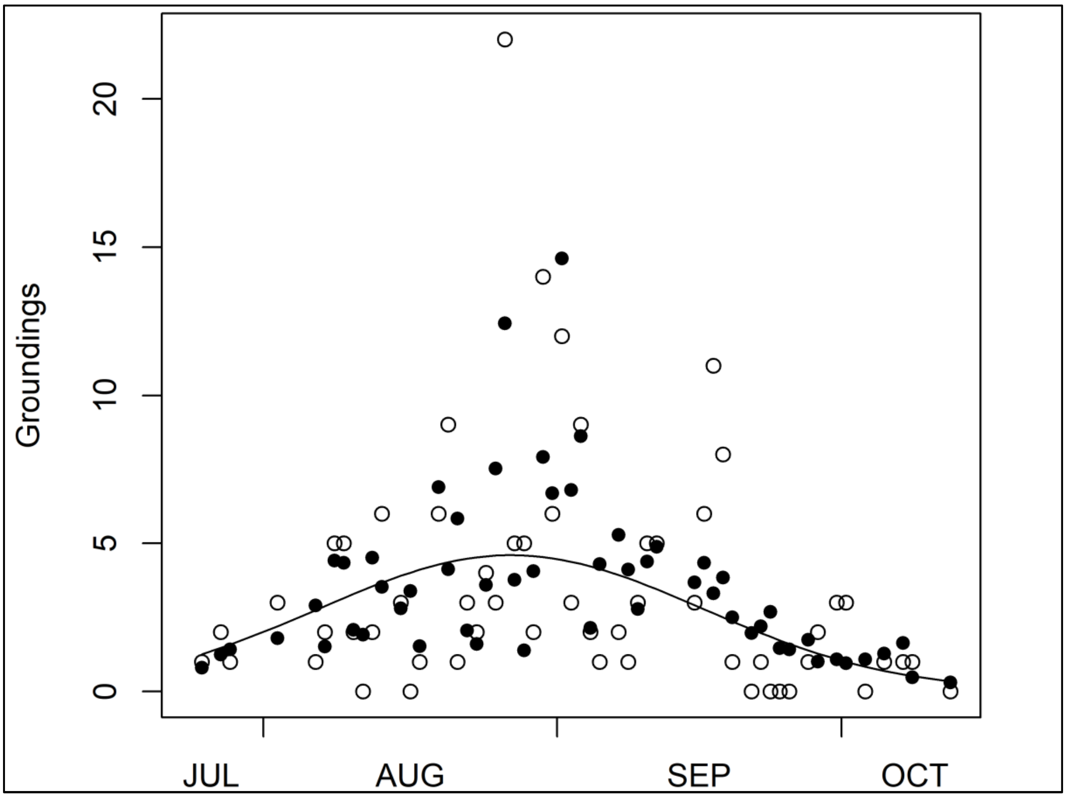

Figure 7: Daily frequency of grounded bats located at the cloister (circles) in relation to fitted values derived from the model in Table 3. The curve shows the significant quadratic trend against date with values for mid-night and daytime activity set at the mean for the period.

Post-mortem results
Post-mortem examinations were carried out on 12 bats recovered from the cloister between 28/07-23/09/2017. Results of the initial histopathology investigation are presented in the appendix.

Some potentially pathological features were seen in the kidney tissues of several of the bats, but no significant findings emerged from further investigation using Periodic acid-Schiff stain, indicating that the features are probably related to immaturity. Sections of the gastro-intestinal tract generally indicated a dearth of ingested material. Further analysis of kidney tissue was carried out for chemical toxin concentration and the results are set out in Table 4. Cadmium concentration is negligible, but there is elevated lead concentration, though not at a level that could be considered clinically significant (Walker *et al.*, 2007). High sodium concentration may be related to the use of formalin fixative.

Table 4: Concentrations of cadmium, lead and sodium in kidney tissues. Sample 1 was taken from 3 of the 6 bats recovered between 28/07-16/08/2017 and Sample 2 from all 6 bats recovered between 30/08-23/09/2017.

	Sample weight (g)	Cd (mg/kg) DWt	Pb (mg/kg) DWt	Na (mg/kg) DWt
Sample 1	0.0167	0.141	15.399	15225
Sample 2	0.0465	0.253	13.522	14497

Discussion
Activity during the swarming period
Roosting within swarming sites
The pattern of bat activity revealed by passive recording within Durham Cathedral cloister highlights a major difference in behaviour from that observed by Sendor (2002) at a comparable swarming site at Marburg Castle in Germany. The latter is not used for roosting during the swarming period, whereas at Durham the peak of activity that consistently occurs just after sunset clearly relates to the emergence of bats roosting within the cloister.

Consequently, the overnight pattern of activity differs from that observed at Marburg, where bats do not begin to enter the site until over two hours after sunset and the volume of activity follows a symmetrical pattern with a peak in the middle of the night (Sendor *et al.*, 2000). During the peak of the swarming season at Durham, activity declines following the post-sunset peak to a plateau extending until after midnight before further decline towards sunrise. Clearly some of this activity must involve bats immigrating into the cloister, since numbers build up through July and August. However, because the entry and exit do not occur through a narrow passage enabling counting using a passive sensor as at Marburg, it is much more challenging to determine the relative contribution to swarming activity of bats roosting at the cloister and those roosting elsewhere.

The reason for the contrast in roosting behaviour between the two sites could conceivably relate to differences in context. At Durham the roosting locations are within and around a 500 year old wooden-beamed ceiling set below a shallow-pitched lead roof that will efficiently conduct radiant heat (Figure 8), whereas the Marburg Castle site comprises a cellar that is open to the outside only through narrow window openings. Since the latter will be substantially buffered from ambient summer warmth, it may be less attractive to newly fledged and still-maturing juvenile bats acclimated to the elevated temperatures that occur within nursery roosts.

Figure 8: View of the cloister from the cathedral's central tower showing the rolled lead sheeting roof over the cloister ranges. Photo by the Revd Peter Barham.

Seasonal trends in swarming activity

Compared to the seasonal pattern of swarming activity observed at the cloister in 2013 (Bell, 2016), there is no indication of a marked peak in activity at the beginning of August followed by a mid-August dip (the presence of which is also suggested in Sendor, 2002 and Sendor *et al.*, 2000), though in both years there is a peak in late August followed by a rapid decline through September. In both Bell (2016) and Sendor *et al.* (2000) there is a suggestion of a short-lived recovery in swarming activity towards the end of September, but this proved to be much more substantial at Durham in 2017 with the seventh highest index of overnight activity occurring on 27/09/2017.

The unusually large late-September peak may have occurred because it followed what appears to be a period of suppressed activity for around 10 days in mid-September (Figure 2), during which practically no activity occurred beyond the post-sunset period. Relatively cool, windy weather during this period may be responsible, commensurate with the general decline of activity detected for all three diurnal time periods with lower temperature and higher wind speeds. A run of days with overnight rainfall during mid-September may also have contributed to the near absence of activity during the mid-night period, for which there is evidence of a negative effect of rain at higher wind speeds.

The failure of the weather-based model to account for the highest levels of activity in late September, despite relatively warm, calm and dry conditions suggests that the late September recovery is real and inadequately modelled by a quadratic temporal trend. If so the occurrence of a late season surge in activity might suggest some re-immigration into swarming sites prior to entry into extended periods of torpor as temperatures decline during October, in which case significant numbers may in fact be present in hibernacula prior to late autumn/early winter immigration.

Effect of the weather on swarming behaviour

Greater activity during warmer, calmer conditions is straightforwardly explained by better feeding conditions created by a greater abundance of flying insects. This might encourage more bats to emerge from roosts, leading to greater post-sunset activity and also free up more time for swarming, leading to greater activity during the mid-night period. If the latter is homologous with the overnight activity observed by Sendor *et al.* (2000), it would primarily involve bats that have journeyed to the swarming site from roosts elsewhere. Deterrence of such journeys on rainy, windy nights might therefore explain the greater predictive power of weather variation in relation to the mid-night period compared to daytime and post-sunset.

It is less straightforward to interpret the effect of wind and temperature on daytime activity, which appears to be confined to the cloister ranges where there are few insects. One possibility is that the bats are flying on relatively warm, calm days to cool down by escaping overheated roosting sites. Speakman (1990) considered this an unlikely explanation for day-flying by common pipistrelles in Britain, but it may be rendered more plausible by thermal environment generated by the lead roofing of the cloister ranges.

Post-swarming activity

The apparent absence of any substantial activity between early October and the end of December is notable in the context of the observations of Racey (1973), Sendor *et al.* (2000) and Korsten *et al.* (2016) suggesting that common pipistrelles vacate swarming sites in early October and then return to hibernate in response to the first frosts of the year. It also contrasts with observations at Durham Cathedral in 2013, which suggested a resumption of activity when overnight temperatures dipped below zero on 19/11/2016 and 22/11/2016 (Bell, 2016) and with remote recording data from the Cathedral in 2010, when several hundred passes were recorded when temperatures dipped below zero on 26-27/11/2010 (Barrett Environmental, 2010).

The Anabat recorders used by Barrett Environmental are designed for use in the open and therefore have a more sensitive microphone setting than the Anabat Roost Logger used in 2017. However, observations in 2013-4 confirm that bats active in winter perform circuits of the cloister ranges and verification procedures carried out in 2017 confirm that bat passes associated with such circuits are recorded by the Roost Logger. On this basis it would seem most likely that there was no influx of bats to the hibernaculum in late 2017 despite the occurrence of several periods of sub-zero night-time temperatures in November and December (Figure 2).

Common pipistrelles are known to visit multiple swarming sites (Sendor, 2002; Korsten *et al.*, 2016), so it may be that bats have adopted an alternative hibernaculum while continuing to visit during the swarming period. Alternatively, bats may have been present but inactive throughout this period, but the fact that no more than a handful of passes was recorded on any night from early October to the end of December (Figure 2) suggests that numbers are small.

Groundings

Mortality rates and foraging efficiency

The very large number of grounded bats that occurred during the swarming period is consistent with findings over a number of years (Bell, 2016) although the figure of 210 probably exaggerates the number involved, as fur-clipping of rehabilitated bats during the 2013 swarming season revealed that repeat groundings were frequent. Nevertheless, the occurrence of such a large number of casualties makes sense only in the context of a rate of mortality somewhere on a gradient between normal levels in a very large population of bats visiting the site and catastrophic mortality on an annual basis in a smaller population which may therefore act as a demographic sink. Determination of where it lies on the gradient must await a reliable estimate of the total numbers of bats visiting the cloister during the swarming season.

Whatever the rate of mortality represented by the numbers involved, the generally emaciated condition of the grounded bats and the apparent lack of gut contents in many of the autopsied individuals, suggests starvation as at least a proximate contributory cause. This is also consistent with the negative relationship between the frequency of groundings and night flying activity, which has been shown to be suppressed during poor weather. High levels of night flying may therefore be taken as proxy of good foraging conditions, during which inefficiently foraging bats are less likely to suffer an energy deficit, which therefore results in fewer groundings. Additional support for a link between groundings and a sub-optimal environment for foraging exists in the form of a negative relationship between the previous night's minimum temperature and the frequency of groundings, since it can be assumed that fewer insects are flying on colder nights.

Environmental factors

The lack of foraging efficiency implied by this evidence may simply be a function of debility related to disease or poisoning by environmental toxins, which would be consistent with an unusually high level of mortality. Observations of bats becoming immediately grounded after emerging from roosting sites could therefore be regarded as significant, as they suggest that grounded bats are primarily those roosting within the cloister, the lead roof of which is a potential source of toxicity. However, post-mortem results indicate a general absence of any signs of disease or clinically significant levels of toxins within the tissues of autopsied bats. Both cadmium and lead were found to be below the critical concentrations expected to cause adverse effects (Cd 105, Pb 25mg/kg dry weight; Walker *et al.*, 2007), although lead concentrations of 13.5 and 15.4 in the two samples are well above the inter-quartile range of a sample of *Pipistrellus* species kidneys from southern England (1.46–4.85), while remaining well below the sample maximum (69.7; Walker *et al.*, 2007). Although this is consistent with contamination related to the roost site, the sub-clinical concentrations suggest that this can be tentatively dismissed as a potential cause of inefficient foraging.

Lack of foraging experience among juveniles

The fact that the vast majority of grounded bats are juveniles suggests that that it might instead relate to inexperience, consistent with the elevated levels of mortality that routinely occur among young animals post-independence. Within this context, the highly significant positive association between day flying and frequency of groundings is notable, since Speakman (1990) speculated that day flying in summer by common pipistrelles is undertaken primarily by juveniles whose inexperience causes inefficient nocturnal foraging, leading to emergence during daylight to make up energy deficits.

At first sight the dearth of insects within the cloister would tend to rule out this theory as an explanation for day flying at the cathedral. However it may be that the bats involved are deterred from venturing beyond the confines of the cloister ranges by the threat of diurnal predators and are engaging in further sub-optimal behaviour commensurate with that leading to the putative energy deficit. On a more speculative level, support for inexperience rather than debility as a cause of inefficient foraging might be inferred from the significant convex quadratic trend in grounding frequency that appears to be independent of the volume of activity within the cloister. The trend rises from near zero in mid-July, peaks at just below five per day in late August, and then declines back to near zero by the end of the swarming period.

In 2013 there was a two week lag between the increase in bat activity within the cloister in early July and the beginning of groundings in mid-July, which might indicate that the beginning of groundings coincides with the appearance of juveniles within the cloister (Bell, 2016). The activity-independent trend in grounding frequency could therefore reflect the proportion of juveniles in the swarming population, though there is no evidence to suggest that this declines from late August onwards. Instead the decline of the activity-independent trend could reflect an improvement in average foraging efficiency among surviving juveniles. Although the evidence for this scenario is currently sparse, it again favours the 'inexperienced forager' hypothesis and the observed relationships of grounding frequency suggest no obvious alternative explanation related to disease or contamination.

As in the model of activity, the combination of a quadratic trend and additional significant variables is inadequate to explain the occurrence of a short term uptick, this time comprising a spike of groundings in mid-September (Figure 7). This occurs towards the end of a period of poor weather and relatively low activity (Figure 2) and may therefore reflect the emergence of severely malnourished bats driven to attempt foraging despite the persistence of sub-optimal conditions.

Conclusions and recommendations

The two main candidate theories to explain the mass groundings and mortalities of juvenile bats that occur most years during late summer/early autumn swarming by common pipistrelles at Durham Cathedral cloister are that they either represent an usually high level of mortality caused by an agent such as disease or an environmental toxin, or that they reflect normal post-fledging mortality among juvenile bats related to their inexperience as foragers. Either could cause individuals to forage inefficiently, for which there is evidence in the form of emaciation and lack of gut contents, as well as the greater frequency of groundings during poor foraging conditions. The absence of significant pathology is more consistent with the 'inexperience' hypothesis, but it would be premature to rule out the possible effect of environmental agents. One reason for this is the use of formalin to preserve the specimens, as this might cause leaching of contaminants from tissues. It would therefore be worthwhile to carry out tests for the presence of toxins in fresh tissue samples from fatalities that occur during future swarming periods at the cathedral.

Uncertainty about the numbers of bats visiting the cloister during the swarming period precludes any strong inferences about the causes of groundings and the associated mortality, since knowledge of the rate of mortality within the population is required to assess whether or not it is unusually high. The indices derived from the Roost Logger provide only a relative measure of bat activity and because common pipistrelles generally roost and hibernate in crevices they are difficult to count even in situations with straightforward access. Counting is therefore all but impossible within the 4m high wooden beamed ceiling of the cloister and the shallow pitched roof space above it.

An alternative approach would involve an assessment of the area from which common pipistrelles immigrate into the cloister. This might be achieved via the attachment of miniaturised radio tags to bats grounded within the cloister prior to their release following rehabilitation. If the number of bats visiting the cloister is large, i.e. thousands rather than hundreds, the bats would be expected to immigrate from a relatively wide area and therefore to disperse widely following release. Such an exercise would also provide some indication of the effectiveness of the rehabilitation process.

Some insight might also be achieved through repeated vantage point surveys of the number of bats emerging from roosting sites within the cloister for comparison with activity indices derived from passive recording. Derivation of a general relationship between the number of bats emerging from cloister roosts and the volume of post-sunset activity might enable ballpark estimation of the numbers active at other times of day, though not the number overall nor the relative contribution of locally roosting individuals, for which the rate of turnover would need to be known. One possible method of quantifying movement in and out would be use of a thermal imaging video camera installed in the 66m central tower of the cathedral with a sufficiently wide-angle lens to cover the entire cloister (Figure 8). However this would almost certainly require the floodlights installed in the cloister to be switched off to enable the movements of individual bats to be picked up from such a range.

Reasons for variation in roosting behaviour between swarming sites can only be tested using between-site comparisons, whereby characteristics that vary among sites are associated with differences in roosting behaviour. However the significance of seasonal trends in swarming activity and frequency of groundings can be clarified by long-term monitoring that records activity data over multiple years. Variation in the response to differences in weather conditions between years would clarify the effects of temperature, wind and rainfall enabling quantification of the underlying weather-independent trends using generalised additive modelling, which in turn would provide clues to their provenance. Long-term data will also be required to clarify the status of the site as a hibernaculum through between-year comparison of over-winter activity variation with weather. However, testing of ideas about the relationship between the frequency of groundings and the proportion of juveniles present or their foraging efficiency and about the occurrence of re-immigration prior to entering torpor would require more intrusive methods involving trapping and examination of bats present at different stages of the swarming period.

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Appendix

Results of initial histopathology investigation. All the bats examined were juveniles.

Recovery			Liver	Kidney	Lungs	Heart	Spleen	Stomach	Intestine
28/07/17	Found dead in cloister - rigor mortis, but absent previous day so probably died overnight	♀	There are variable autolytic changes. Some slight dilatation of sinusoids is seen but no significant hepatocyte changes.	Amorphous eosinophilic droplets are seen in dilated Bowman's capsules in many glomeruli.	These are congested with some artefactual collapse.	No significant findings.	Significant autolysis is seen.	This is well preserved but no significant findings.	There is more significant autolysis and only scant contents seen.
29/07/17	Found dead in cloister - some rigor mortis, but obviously trodden on & fresh entrails extruded.	♂	There was no liver section on prepared slide.	There are more localised glomerular changes as seen above. Slightly basophilic flocculent material is seen in many tubules.	These are very congested with artefactual collapse. There is possible slight increase in cellularity but probably an artefact.	No significant findings.	The red pulp is very congested.		This is generally well preserved with prey material seen in lumen. A couple of cross-sections of possible nematodes are seen but with little associated pathology.
03/08/17	Found grounded in cloister. In poor condition, so probably grounded 1 day +. Died in captivity 04/08/2017.	♀	There is variable autolysis but with no significant findings.	There are changes similar to the above.	Again congestion and a degree of artefactual collapse is seen.	No significant findings.	No section.		There is variable autolysis and scant contents.

Recovery			Liver	Kidney	Lungs	Heart	Spleen	Stomach	Intestine
09/08/17	Found dead in cloister - rigor mortis but recent. Forearm 32mm, weight 3.67g	♂	There is slight dilatation of the sinusoids and scattered hepatocyte necrosis/autolysis is seen.	Similar changes as previous cases.	There is variable autolysis, slight congestion but no significant findings	There is variable autolysis but no significant changes.	No significant findings.	There is generally scant contents and a single cross section of a possible helminth is seen.	
09/08/17	Found dead in cloister - rigor mortis but recent. Forearm 33mm, weight 3.84g	♀	There are areas of autolysis but the well preserved parts show no significant findings.	Part is autolysed but the glomeruli are congested with droplets in Bowman's space and flocculent material in many tubules.	There is slight congestion but no significant findings.	No significant findings.	No significant findings.	This is well preserved but little contents seen.	There is variable autolysis and some contents seen.
16/08/17	Found dead in cloister - very fresh. Forearm 33.5mm, weight 4.03g.	♀	This is slightly autolysed but no significant findings.	There is glomerular congestion but very limited capsular distension. Some basophilic droplets are seen in the tubules.	There is variable autolysis but no significant findings.	No significant findings.	No significant findings.		There were areas of extensive autolysis but in better fixed parts no significant findings were seen.

Recovery			Liver	Kidney	Lungs	Heart	Spleen	Stomach	Intestine
30/08/17	Found alive in cloister, died shortly afterwards. Forearm 33mm, weight 4.01g.	♀	Unremarkable.	There is a degree of autolysis. Wispy pale eosinophilic contents in tubules.	These are congested with very limited hyperplasia of bronchiolar epithelium and swelling of arteriolar endothelial cells. There is some artefactual collapse and possibly a limited focal mononuclear increase in cellularity.			Unremarkable except lack of feed contents.	
30/08/17	Found dead in cloister. Forearm 31.5mm, weight 3.35g	♂	Unremarkable.	Pale flocculent material is seen in many glomeruli.	There is moderate congestion and artefactual collapse of alveoli.			There is a moderate degree of autolytic change. Little feed is seen and a cross section of a female possible nematode.	
02/09/17	Found alive in cloister, died shortly afterwards. Forearm 33mm, weight 4.04g.	♂	A degree of autolysis is seen otherwise unremarkable.	No kidney seen on this slide.	These are congested and slightly collapsed.				
09/09/17	Found dead in cloister. Forearm 33mm, weight 3.84g.	♀	Numerous sections but unremarkable except for autolytic changes.	No kidney seen on this slide.	These are congested and slightly collapsed.			Unremarkable.	

Recovery			Liver	Kidney	Lungs	Heart	Spleen	Stomach	Intestine
17/09/17	Found alive in cloister, died shortly afterwards. Forearm 33.5mm, weight 4.13g.	♀	Unremarkable.	Some flocculent material is seen in glomeruli.	These are congested with some artefactual collapse.			A cross section of possible nematode is seen.	
23/09/17	Found dead in cloister. Forearm 31mm, weight 3.64g.	♂	Unremarkable.	Some flocculent material is seen in glomeruli.	These are congested with some artefactual collapse.			A cross section of possible nematode is seen.	