Autumn swarming behaviour of Natterer’s bats in the UK: Population size, catchment area and dispersal

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ABSTRACT

Many species of temperate bats visit underground sites in autumn, prior to hibernation, and chase each other in and around the entrances in an event known as autumn swarming. It has been suggested that swarming is a mating event that facilitates gene flow between bats from otherwise isolated summer colonies. We describe swarming behaviour at a cluster of four caves in the North of England and provide direct evidence for seasonal migration of Natterer’s bats (Myotis nattereri) between these caves and many summer nursery roosts in a catchment area of at least 60 km radius. Mark-recapture analysis suggests that an estimated 2000–6000 Natterer’s bats use the three best-studied caves, together with smaller numbers of four other species: M. daubentonii, M. brandti, M. mystacinus and Plecotus auritus. Recaptures also show that there is a small interchange of bats between these three caves, which are 0.6–1.5 km apart. Capture rates, automatic logging and video recordings at one cave suggest that an average 310–400 bats visit the cave each night. Mating at swarming sites would be particularly important for gene flow if a species showed no other dispersal pattern. We provide evidence for natal philopatry, with little or no dispersal, in both sexes of Natterer’s bats. The protection of swarming sites is discussed in light of our findings.

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1. Introduction

Many animals in a range of taxa change their location and social groupings through the year for ecological and life history reasons: as a response to changes in environmental temperature and resource availability, to avoid predators and competition and to find mates (Pusey, 1987; Fryxell and Sinclair, 1998). Bats are no exception to this. Many species of temperate bat spend the summer in small to medium sized colonies (approximate range 10–1000 individuals), usually roosting in buildings or trees. The sexes are often segregated with females and young in nursery roosts and males roosting nearby in solitary or group roosts. In the winter when food abundance is low, both sexes move to hibernacula, often caves and mines, which provide a stable temperature for hibernation (Altringham, 1996; Speakman and Thomas, 2003). Ringing (or banding) and molecular studies in North America and Europe show that some bats migrate up to hundreds of kilometres from several summer roosts to caves and mines, which can be limited in number in some areas (Davis and Hitchcock, 1965; Griffin, 1970; LaVal and LaVal, 1980; Altringham, 1996; Petit and Mayer, 2000; Fleming and Eby, 2003).

Movements and activities during autumn and spring, however, have not always been taken into account in describing the life-histories of temperate bats. The observation that large numbers of bats also visit caves and mines in autumn, a few months prior to hibernation, was first described in North America in the 1960s and was termed autumn (or fall)
swarming’ (Davis, 1964; Davis and Hitchcock, 1965; Fenton, 1969). Swarming involves bats chasing each other in and around cave entrances, rather than just entering the cave for roosting purposes (Fenton, 1969; Mumford and Whitaker, 1975; Cope and Humphrey, 1977; LaVal and LaVal, 1980; Parsons et al., 2002). Several reasons have been proposed to explain swarming, including assessing suitable hibernacula (Davis and Hitchcock, 1965; Rehák et al., 1994) or showing juveniles the location of such hibernacula (Fenton, 1969). However, the most favoured explanation (Fenton, 1969; Humphrey and Cope, 1976; Furmankiewicz and Górniak, 2002; Parsons et al., 2002), supported by some genetic (Kerth et al., 2003; Veith et al., 2004; Rivers et al., 2005) and behavioural evidence (Fenton, 1969; Barclay and Thomas, 1979; Thomas et al., 1979; LaVal and LaVal, 1980; Kerth et al., 2003), is that swarming is a mating event which could allow gene flow between bats from otherwise isolated summer colonies. However, although bats from several summer colonies can hibernate together, movement of both sexes for mating purposes (breeding dispersal) is uncommon in mammals (Greenwood, 1980), and the evidence that bats are swarming together, and therefore mating, from many summer colonies is limited. The evidence to date is based on a few studies showing recaptures from up to three summer roosts (Humphrey and Cope, 1976; Bauerová and Zima, 1988; Parsons and Jones, 2003), and molecular studies providing indirect evidence that swarming bats have come from more than one colony (Kerth et al., 2003; Veith et al., 2004).

There are still many gaps in our understanding of the role swarming plays in the seasonal movements of bats and the structure of the bat populations. Mating of bats from different colonies at swarming sites would be especially important for gene flow and the prevention of inbreeding (and the likely concomitant loss of individual fitness) if both sexes were philopatric and therefore did not mix at other times. Juvenile dispersal of at least one sex from the natal site has evolved in many taxa to avoid problems of inbreeding and competition which could arise from philopatry (Moore and Ali, 1984; Pusey, 1987). In mammals, males are usually the dispersing sex and in birds it is usually females (Greenwood, 1980; Pusey, 1987). Female philopatry to the natal colony has been shown in several temperate bat species (e.g. Kurta, 2002). However, male dispersal is more difficult to assess as males are harder to find if they do not roost in the main nursery roost. Ringing and molecular studies have revealed that in some species (e.g. Nyctalus noctula in Europe) females are philopatric and males disperse (Petit and Mayer, 2000; Petit et al., 2001) and in other species (e.g. Rhynchonycteris naso and Balantiopteryx plicata) both sexes have been shown to disperse (Bradbury and Vehrencamp, 1977). Differences in dispersal strategy may depend on parental investment (Bradbury and Vehrencamp, 1977), food availability, territory/home range availability, and roost limitations, as well as the need to prevent inbreeding.

The Natterer’s bat (Myotis nattereri) is a swarming species which spends the summer in trees and buildings, usually sexually segregated, and hibernates in caves and mines during the winter (Gilbert and Stebbings, 1958; Altringham, 2003). In the summer, females, juveniles and sometimes adult males roost in nursery roosts though males typically roost nearby, singly or in small groups (Cerveny and Horácek, 1981; Park et al., 1998; Smith, 2000). The species is widespread in Europe, but scarce throughout its range.

This paper addresses the following primary questions and discusses the answers with regard to bat conservation:

- Are male and female Natterer’s bats philopatric or is there permanent dispersal from the natal colony of at least one sex?
- Do Natterer’s bats make seasonal movements from many summer roosts to the same autumn swarming site?
- How many bats visit a swarming site and from how large a catchment area?
- Do bats visit more than one swarming site?
- How many bats visit a swarming site on each night?

2. Methods

2.1. Study site

Bats were captured at a cluster of four autumn swarming caves called The Ryedale Windy Pits and at 11 surrounding summer nursery roosts in North and East Yorkshire, UK (Fig. 5). Slip Gill, Antofts, Bucklands and Ashberry were chosen as the main study caves because large numbers of bats had been observed using these caves in autumn. They are vertical or near-vertical fissures in Corallian Jurassic limestone resulting from mass sliding movements of the bedrock. The pits are between 170–366 m long and 38–43 m deep with entrances approximately 1–3 m across, and are all located on steep wooded slopes (Cooper et al., 1976, 1982) within 0.5–3.0 km of each other. The land in the valley bottom and on the surrounding low hills is mixed woodland, pasture and arable fields. They are within the North York Moors National Park and protected as Sites of Special Scientific Interest (SSSI).

2.2. Capture methods

Bats were captured at the Windy Pits between mid-August and mid-November to coincide with the UK autumn swarming season, using harp traps (Austbat, Australia) and mist nets (North Ronaldsay superfines, BTO) outside the cave entrances (Slip Gill, 1997–2003, other Windy Pits 2001–2003). Each cave was visited no more than once per week and entrances were only partially enclosed to avoid excessive disturbance. Bats at summer roosts were captured once or twice per year between June and mid-August 2002–2003 using static hand nets outside roost exits.

All bats were identified to species and sex, and reproductive condition was recorded. The bats were aged as adults or juveniles (born that summer) according to the degree of ossification of the epiphyseal joints in the finger bone (Racey, 1974; Anthony, 1988). This was not always possible in autumn when the joints begin to fuse, so bats were classified as adults if age was uncertain. Natterer’s bats were ringed with a 2.9 mm aluminium bat ring (The Mammal Society, UK). All procedures were carried out under licences from English Nature. All bats were released at the point of capture.
Two additional methods were used to monitor and count bats at Slip Gill. Visual counts of bats going in, out and approaching (approximately 2 m) the cave were recorded per minute from sunset for 3 h 30 min using a nightscope (Dedal D-220 Ultra, generation 2) with supplementary light from an infra-red lamp. Activity during the following 3 h 20 min was recorded using a video-recorder (Sony Handycam Digital Hi-8) with the nightscope attached to the lens. This was the time of peak activity and was recorded on video for later analysis. Observations and recordings were made on 10 nights, usually once a week between 4th September and 20th November 2003.

The number of bats visiting Slip Gill during the 2003 swarming season was also recorded using an automatic logger. This consisted of a waterproof box containing a heterodyne bat detector (Batbox III, Batbox Ltd), a counter to convert a bat pass into a single pulse (Skye Instruments), and a count logger that stored bat passes per minute (Gemini Data Loggers). The logger was placed 1 m outside the entrance to Slip Gill for between 3 and 6 days each week for 6 weeks from 24th September 2003 (14 nights in total after removing nights on which rain was recorded). These data were categorised into 30 minute time periods and compared with capture data from 22 nights at Slip Gill during the 1998–2003 swarming seasons. Ashberry Windy Pit was excluded as there were very few capture nights with good weather at this site.

### Population estimate

The population size and survival estimate of the bats using the Windy Pits was estimated using a simple Jolly-Seber mark-recapture method computed by JOLLY 3 (Jolly, 1965; Hines, 1988). Model A was used which allows both death and recruitment. The model assumes complete mixing i.e. that every individual has the same chance of being captured on any given capture event. To meet this assumption, the data were grouped into years rather than nights, with each year being one capture event. This was because recaptures indicate that bats are unlikely to visit a swarming site every night within a season. Only data from male Natterer’s bats captured at Slip Gill from 1998 to 2003 were used because it was the only site with sufficient data for a reliable estimate. Females were not included as the capture and recapture rates were too low for analysis. The small numbers of bats captured in the spring or recaptured at other sites were excluded for simplicity. The population estimate of the number of male Natterer’s using Slip Gill was then extrapolated to provide estimates for the total number of Natterer’s bats and other bat species using Slip Gill, Bucklands and Antofts. The population estimate will therefore contain some error but extrapolating from the largest dataset was deemed the best approach as the Jolly estimate is usually only reliable when 9% or more of the population is sampled (Thomas, 1988).

### Assessing philopatry

To assess levels of philopatry in Natterer’s bats, data from a bat box scheme in Wareham Forest in Dorset, England (Fig. 5) were analysed. This data set, covering the period from 1977 to 1993, is the best information available on the movements of both adult and juvenile Natterer’s bats in the UK. The scheme was managed by the Forestry Commission and included approximately 500 boxes in 20 sites covering 360 km² (for further details see Park et al., 1998). Four surveys were conducted between March and October each year. Bats were ringed and any recaptures were recorded. Distances between adjacent sites varied from 0.5 to 2.5 km, with a mean (±SD) separation of 1.6 ± 0.5 km. The analysis assesses movements between sites not boxes within sites.

### Results

#### Swarming captures

Six species were captured at the Ryedale Windy Pits between 1997 and 2003 (Table 1). Not all species were ringed and so the following figures include recaptures. The majority of the captures were Natterer’s bats (M. nattereri), followed by brown long-eared bats (Plecotus auritus). Also captured in low numbers were the Myotis species; Daubenton’s (M. daubentonii), Brandt’s (M. brandtii) and whiskered bats (M. mystacinus); and two 45 kHz pipistrelle bats (Pipistrellus pipistrellus). In all species the sex-ratio was skewed towards males, with the overall mean sex-ratio of 74.5% males and 25% females (0.5% unknown due to escape before sexing) showing significant departure from 1:1 (Table 1, $\chi^2 = 361.07$, d.f. = 1, $p < 0.01$). There was no significant variation in sex-ratio across species (contingency $\chi^2 = 6.57$, d.f. = 4, $p = $ ns, the sample size for P. pipistrellus was too small to include in this test).

<table>
<thead>
<tr>
<th>Sex</th>
<th>Myotis nattereri</th>
<th>Myotis daubentonii</th>
<th>Myotis mystacinus</th>
<th>Myotis brandtii</th>
<th>Plecotus auritus</th>
<th>Pipistrellus pipistrellus</th>
<th>Total</th>
<th>Total sex ratio (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>882 (75.8%)</td>
<td>66 (75.0%)</td>
<td>17 (58.6%)</td>
<td>14 (73.7%)</td>
<td>116 (68.2%)</td>
<td>2 (100%)</td>
<td>1097</td>
<td>74.5</td>
</tr>
<tr>
<td>Female</td>
<td>280 (24.1%)</td>
<td>22 (25.0%)</td>
<td>12 (41.4%)</td>
<td>5 (26.4%)</td>
<td>49 (28.8%)</td>
<td>0</td>
<td>368</td>
<td>25.0</td>
</tr>
<tr>
<td>Unk</td>
<td>2 (0.2%)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5 (2.9%)</td>
<td>0</td>
<td>7</td>
<td>0.5</td>
</tr>
<tr>
<td>Total</td>
<td>1164 (79.1%)</td>
<td>88 (6.0%)</td>
<td>29 (2.0%)</td>
<td>19 (1.3%)</td>
<td>170 (11.5%)</td>
<td>2 (0.1%)</td>
<td>1472</td>
<td>100</td>
</tr>
</tbody>
</table>

Unk = unknown.
3.2. Seasonal swarming patterns

Swarming activity was observed from mid-August until mid-November, peaking mid-September to mid-October, but there was considerable variation in the numbers of bats captured from night to night (Fig. 1). The numbers of bats captured were comparable across sites and across years.

On each survey night in September and October 2003, the number of bats entering Slip Gill (based on night video recording) was not significantly different from the number of bats exiting (Fig. 2; 4th September, $\chi^2 = 0.04$; 12th September $\chi^2 = 0.68$; 18th September $\chi^2 = 0.88$; 24th September $\chi^2 = 3.80$; 1st October $\chi^2 = 3.80$; 17th October $\chi^2 = 4.23$; 23rd October $\chi^2 = 1.57$; 30th October $\chi^2 = 0.37$; for all dates d.f. = 1 and $p = \text{ns}$ after a sequential Bonferroni correction). On both survey nights in November 2003, total activity levels had decreased, but significantly more bats entered Slip Gill than exited (Fig. 2; 6th November, $\chi^2 = 8.17$; 20th November, $\chi^2 = 24.34$; for both dates d.f. = 1 and $p < 0.05$ after a sequential Bonferroni correction). Several winter searches found fewer...
than 10 of these crevice-dwelling species on any one visit, however up to 50 bats were observed leaving Slip Gill on two nights in April.

The numbers of bats observed entering, exiting and approaching the cave were also used as indices of activity. They suggest that swarming activity peaks in late September to October (Fig. 2), though these data are from just one cave in one year. The observation that there are sometimes more approach flights than flights entering or exiting (Fig. 2) indicates that bats fly around the entrance, often several times, before entering. Some bats may not even enter the cave.

### 3.3 Nightly swarming patterns

The nightscope observations show that most bats entered Slip Gill and then left in the same evening (Figs. 2 and 3), however there is evidence that small numbers of bats roost there throughout the swarming season. This is indicated by a small early peak of emergence from the cave. The most extreme example observed, on one night in October (Fig. 3, see also early peaks in Fig. 4), corresponds to the average roost emergence time of 30–60 min after sunset for Natterer’s bats (Swift, 1997; Siemers et al., 1999; Smith, 2000).

The peak time for swarming as determined by both loggers (Fig. 4a) and captures (Fig. 4b) was 4–6 h after sunset with most bats arriving at Slip Gill from elsewhere. The pattern of activity recorded by the two methods was similar, for times when both methods were used concurrently to count bats (to 7 h after sunset).

We can use Figs. 1, 2 and 4 to estimate how many bats (all species) visit Slip Gill on an average night between late August and early November. The mean (±SD) number of bats captured per night was 36 ± 30 \( (n = 22, \text{range 4–123, Fig. 1}) \), which will be an underestimate of the number of bats present as not all bats would have been captured. Nightscope observations suggest that about 10% of the approaches to a harp trap resulted in capture, which would give us an estimate of 360 bats visiting Slip Gill on one night, or more likely 400 as we did not catch for the entire night. The mean (±SD) number of bats observed flying in or out of Slip Gill per night was 295 ± 273 \( (n = 10, \text{range 34–840, Fig. 2}) \). Of the bats approaching may not enter the cave so the estimate is 300–400 bats present. The mean (±SD) number of bats recorded per night using the automatic logger was 1199 ± 1070 \( (n = 14, \text{range 248–4353, Fig. 4a}) \), which will be an overestimate as bats can be counted more than once as they fly in, out and approach the cave. Data from the nightscope observations suggest that the mean total number of passes in, out and approaching \( (1178 ± 976, n = 10, \text{range 395–3389, Fig. 2}) \) is 3.8 times the number of bats going in or out. If this ratio is used on the logging data, the number of bats going in or out would be 316 \( (1199/3.8) \), but again some bats may not enter the cave. All methods therefore lead us to conclude that on an average swarming night approximately 310–400 bats are present.

### 3.4 Recaptures and movements between swarming caves

Table 2 shows the number of Natterer’s bats ringed at the Windy Pits and at the surrounding summer roosts. As previously shown, the majority of the bats captured at the Windy Pits were males. The majority of the captures at summer sites were adult females, but juveniles of both sexes and a few adult males were also ringed. The sex-ratio of adults in the summer roosts was heavily skewed towards females (3.2% males: 96.8% females, \( \chi^2 = 217.03, \text{d.f.} = 1, p < 0.001 \)) but the sex-ratio of the juveniles did not depart from 1:1 (45.6% males: 54.4% females, \( \chi^2 = 0.79, \text{d.f.} = 1, p = \text{ns} \)).

Although most Natterer’s bats were recaptured at the Windy Pit at which they were originally ringed, there was some movement of bats between Windy Pits (Table 3). Five of the 129 (3.9%) recaptured bats moved cave. Movements occurred between all three main caves and one movement occurred within a night. The proportion of recaptures increased with the number of ringed bats at each site. The proportion of females recaptured was significantly lower than the proportion of males recaptured across all Windy Pits (Table 4, \( \chi^2 = 17.82, \text{d.f.} = 1, p < 0.001 \)). There was no difference in the proportion of males and females recaptured across Windy pits (Table 4, contingency \( \chi^2 = 0.13, \text{d.f.} = 2, p = \text{ns} \)).
3.5. Catchment area

Recaptures of ringed Natterer’s bats were made between the Windy Pits and eight summer locations in a radius of over 60 km (Fig. 5, Table 4). Movements were made to and from the Windy Pits, by adults and juveniles of both sexes (Table 4). Most recaptures were between a Windy Pit and a known summer roost, though three bats were found dead by members of the public (Fig. 5, Table 4). Two of these individuals were ringed on the same night at Slip Gill (consecutive ring numbers) and may be from the same colony since they were found close together in the summer.

3.6. Population estimate

The population size of male Natterer’s visiting Slip Gill per year estimated from the mark-recapture model was 681 (372–991) (mean with 95% confidence intervals). Assuming a 1:1 sex-ratio in the population as a whole, the total estimate of male and female Natterer’s visiting Slip Gill would be
approximately 1400, with a range of about 750–2000. As capture rates at Slip Gill, Bucklands and Antofts are comparable (Fig. 1), the estimated number of Natterer’s bats using all three Windy Pits will be three times this number: approximately 4000, with a range of 2000–6000. Natterer’s bats account for 79% of all captures, so the estimated number of bats of all species using the three Windy Pits is approximately 5000 (range 3000–7500). However if sex-ratio in the population is not considered, the estimated number of bats using all three Windy Pits will be approximately 6000, with a range of 3000–9000.

### Table 2 – The number of Natterer’s bats ringed at swarming and summer sites

<table>
<thead>
<tr>
<th>Site name</th>
<th>Adults</th>
<th>Juveniles</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Female</td>
</tr>
<tr>
<td>Windy Pit swarming caves</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antofts</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>Bucklands</td>
<td>124</td>
<td>60</td>
</tr>
<tr>
<td>Slip Gill</td>
<td>165</td>
<td>36</td>
</tr>
<tr>
<td>Total</td>
<td>307</td>
<td>98</td>
</tr>
<tr>
<td>Swarming total</td>
<td>1011</td>
<td>247</td>
</tr>
<tr>
<td>Summer roosts</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ellerburn</td>
<td>64</td>
<td>31</td>
</tr>
<tr>
<td>Hamsterley</td>
<td>33</td>
<td>28</td>
</tr>
<tr>
<td>Kirkburn</td>
<td>28</td>
<td>18</td>
</tr>
<tr>
<td>Kilnwick</td>
<td>23</td>
<td>14</td>
</tr>
<tr>
<td>Low Catton</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>Long Newton</td>
<td>73</td>
<td>60</td>
</tr>
<tr>
<td>Summerbridge</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>South Cave</td>
<td>13</td>
<td>11</td>
</tr>
<tr>
<td>Wintringham</td>
<td>56</td>
<td>36</td>
</tr>
<tr>
<td>Woodfield</td>
<td>16</td>
<td>7</td>
</tr>
<tr>
<td>Summer total</td>
<td>351</td>
<td>240</td>
</tr>
</tbody>
</table>

The number of juveniles at swarming sites will be an underestimate as it is difficult to distinguish juveniles in the autumn.

### Table 3 – Recaptures between Windy Pit caves

<table>
<thead>
<tr>
<th>Windy Pit</th>
<th>Sex</th>
<th>Total ringed</th>
<th>Total recaptured</th>
<th>Original ringing location of recaptures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Same Windy Pit</td>
<td>Different Windy Pit</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antofts</td>
<td>m</td>
<td>178</td>
<td>17 (9.6%)</td>
<td>15 (88.2%)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>68</td>
<td>1 (1.5%)</td>
<td>1 (100%)</td>
</tr>
<tr>
<td>Bucklands</td>
<td>m</td>
<td>128</td>
<td>9 (7%)</td>
<td>9 (100%)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>36</td>
<td>1 (2.8%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td>Slip Gill</td>
<td>m</td>
<td>431</td>
<td>89 (20.6%)</td>
<td>88 (98.9%)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>156</td>
<td>12 (7.7%)</td>
<td>11 (91.7%)</td>
</tr>
<tr>
<td>Total</td>
<td>m</td>
<td>737</td>
<td>115 (15.6%)</td>
<td>112 (97.4%)</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>260</td>
<td>14 (5.4%)</td>
<td>12 (85.7%)</td>
</tr>
</tbody>
</table>

A = Antofts, B = Bucklands, SG = Slip Gill. Distance between Windy Pits: SG to A = 0.9 km, SG to B = 1.5 km, A to B = 0.6 km.

### Table 4 – Movement of Natterer’s bats in the catchment area of the Windy Pits

<table>
<thead>
<tr>
<th>Location and date of ringing</th>
<th>Location and date of recapture</th>
<th>Sex and age when ringed</th>
<th>Direct distance (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slip Gill 17/09/99</td>
<td>South Cave 22/07/02</td>
<td>Adult female</td>
<td>63</td>
</tr>
<tr>
<td>Ellerburn 06/08/02</td>
<td>Slip Gill 11/09/02</td>
<td>Juvenile female</td>
<td>26</td>
</tr>
<tr>
<td>Woodfield 06/08/02</td>
<td>Antofts 15/09/02</td>
<td>Juvenile male</td>
<td>43</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Slip Gill 28/09/03</td>
<td>Adult female</td>
<td>25</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Antofts 21/09/03</td>
<td>Juvenile female</td>
<td>25</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Slip Gill 28/09/03</td>
<td>Adult male</td>
<td>25</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Slip Gill 28/09/03</td>
<td>Adult female</td>
<td>32</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Slip Gill 28/09/03</td>
<td>Adult male</td>
<td>11</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Slip Gill 28/09/03</td>
<td>Adult male</td>
<td>10</td>
</tr>
<tr>
<td>Wintringham 11/08/02</td>
<td>Slip Gill 28/09/03</td>
<td>Adult male</td>
<td>13</td>
</tr>
</tbody>
</table>
is genuinely skewed (76% males: 24% females) the estimate would be approximately 2500 Natterer’s bats and 3200 bats of all species using the three Windy Pits.

The mean survival estimate from the mark-recapture model was 0.86 (0.66–1.00). This suggests approximately 50% survival to 5 years with some bats living over 10 years. Ringing recaptures suggest this is reasonable and it is within the range of reported values, but at the higher end of this range (Tuttle and Stevenson, 1982). It may be slightly overestimated as the data do not include juveniles which do not survive to their first swarming season.

3.7. Philopatry

Table 5 summarises data from the Wareham bat box scheme. The proportion of bats that were recaptured at all was higher for females than males in both age classes (adults, \( \chi^2 = 7.28, \) d.f. = 1, \( p < 0.01; \) juveniles, \( \chi^2 = 10.40, \) d.f. = 1, \( p < 0.01 \)). Of the Natterer’s bats ringed as juveniles and recaptured as adults, none was recaptured at a site different from its natal site (Table 5). Of those bats first ringed as adults, only one male (1.6%) and five females (3.7%) changed site. Five out of six of these movements were from two boxes at one site the day after they were surveyed, so it is probable the movements were caused by human disturbance. The remaining movement was one adult female which moved 2.5 km, within the observed average home range of a Natterer’s bat (Siemers et al., 1999; Smith, 2000). These data suggest that permanent dispersal is low in both sexes of Natterer’s bats.

4. Discussion

4.1. Which species swarm?

The bats caught at the Windy Pits were predominantly Myotis species, as seen in most swarming studies in Europe and North America (e.g. LaVal and LaVal, 1980; Parsons et al., 2002). Species composition depends on geographic location and the Windy Pits may have few \( M. \) brandti and \( M. \) mystacinus because they are close to the northern edge of their range. \( M. \) nattereri was the most common swarming species, but \( M. \) daubentonii and \( P. \) auritus were caught in significant numbers.
4.2. Why is the sex-ratio and recapture rate biased towards males?

The sex-ratio was found to be biased towards males in all species, as observed in most swarming studies (Davis and Hitchcock, 1965; Humphrey and Cope, 1976; Bauerová and Zima, 1988; Parsons et al., 2002; Kerth et al., 2003). The recapture rate at swarming sites was also higher for males than females, as was found for M. nattereri and M. daubentoni by Parsons et al. (2002) and M. sodalis in the USA (LaVal and LaVal, 1980). The sex-ratio may be truly biased towards males or result from behavioural differences during swarming. Spring-emergence sex-ratio may provide a better indication of the true sex-ratio, though some species show swarming behaviour in the spring (e.g. P. auritus, Furmankiewicz and Górniak, 2002). A study of Natterer’s bats in Poland showed that sex-ratio was significantly biased towards males during autumn swarming but returned to unity in spring-emerging bats (Furmankiewicz and Górniak, 2002). This, combined with the fact that juvenile sex-ratio did not depart from unity in this study, suggests that the actual sex-ratio in Natterer’s bats is 1:1.

It has been suggested that a male-biased sex-ratio and more male recaptures at swarming sites is a result of females going straight into hibernation after copulation at swarming sites while males remain active at the cave in order to achieve more copulations (Cope and Humphrey, 1977; LaVal and LaVal, 1980). The only evidence is from a study of M. griseescens which shows the sex-ratio of hibernating bats to fall from 99% female to 41% female over the course of the swarming season (Tuttle, 1976). Males generally have more to gain from multiple copulations than females (Bateman, 1948; Anderson, 1994) and should benefit from prolonged swarming activity.

4.3. When is the swarming season?

Swarming was observed from mid-August to mid-November which is at the later end of the swarming seasons observed in a number of studies in Europe and North America which range from July to November (Davis, 1964; Hall and Brenner, 1968; Mumford and Whitaker, 1975; Cope and Humphrey, 1977; Furmankiewicz and Górniak, 2002; Parsons et al., 2003). The large night-to-night variation in activity has also been seen in other studies (Humphrey and Cope, 1976) and is at least partly explained by variation in weather (Fenton, 1969; Parsons et al., 2003).

4.4. Do bats stay to hibernate at their swarming cave?

The nightscope observations show that most bats visiting Slip Gill leave during the same night, but that later in the season there is a net influx into the cave, with about twice as many bats entering as leaving, suggesting at least some bats stay to hibernate. This is supported by the observation of bats exiting Slip Gill in spring. Studies in Europe also found evidence of spring emergence and some suggestion of an autumn influx (Bauerová and Zima, 1988; Rehák et al., 1994; Degn et al., 1995); Fenton (1969) found that bats significantly increased the length of time they stayed in the swarming mine per night as the season progressed.

Few hibernating bats were found during visual searches of the Windy Pits in winter. Natterer’s bats are crevice dwellers (Cerveny and Horáček, 1981; Furmankiewicz and Górniak, 2002) and can therefore be difficult to find in caves. Similar results of high numbers of Natterer’s bats in the autumn and spring, but not in winter, have been found in other studies (Gilbert and Stebbings, 1958; Rehák et al., 1994; Furmankiewicz and Górniak, 2002; Parsons et al., 2002).

4.5. What time of night do bats swarm and where do they come from?

Swarming activity in this study peaked 4–6 h after sunset whether assessed by number of captures or by logging activity. The late peak in activity supports the idea that most bats are arriving at the swarming cave either from distant locations, or after foraging in the early evening when insects are most abundant. The frequent occurrence of a small, early peak in emergence shows that a small number of bats do roost in the swarming cave. Similar late activity, with a variable number of bats day-roosting in the swarming cave has been seen in other studies (Davis and Hitchcock, 1965; Hall and Brenner, 1968; Degn et al., 1995). Ringing has shown that some species e.g. M. lucifugus, M. griseescens and M. sodalis, return to their summer roost during the swarming season (Davis, 1964; Tuttle, 1976). A radio-tracking study on M. nattereri and M. daubentoni found that bats roosted 0.1–26.7 km from the swarming site (Parsons and Jones, 2003).

4.6. Are bats faithful to one swarming cave?

Previous studies have suggested that bats are faithful to swarming sites, based on a small number of recaptures (LaVal and LaVal, 1980) and on radio-tracked bats in which only a small proportion returned to any cave (Parsons and Jones, 2003). Our results show that although most recaptures are made at the site of original capture, some bats do visit more than one cave. Because of the short distances between the Windy Pits (<2 km to nearest neighbour), they could be collectively considered as a single swarming ‘area’. We captured at two sites simultaneously on only three occasions, and our single recapture between two sites on one of these nights indicates movements between sites may be underestimated. Studies of M. lucifugus showed that some bats returned to the same swarming cave year after year but a small number moved up to 106 km. This tended to be between years, with very few examples within years (Fenton, 1969; Humphrey and Cope, 1976).

4.7. What is the catchment area of the Windy Pits?

Recapture of ringed bats shows that the catchment area of the Windy Pits is large, extending at least 63 km to the south-east. They are the longest caves in this cave-poor region, so it is unsurprising that there were recaptures from distant sites. Many summer roosts remain undiscovered and ringing has been carried out for only a short time, so the catchment area is almost certainly under-estimated. The movement of over 60 km from Slip Gill to South Cave is the longest published
for a Natterer’s bat. Studies of Natterer’s bats in the summer show that this small species does not usually travel far. The average foraging range is 1.0–4.4 km from their roost (Siemers et al., 1999; Smith, 2000), but the average flight speed is 15.5 km/h (Siemers et al., 1999), so they are clearly capable of flying long distances in a short time. Although bats usually forage close to their roost site, migration studies show bats are capable of flying much greater distances relatively quickly (e.g. Davis and Hitchcock, 1965).

4.8. Do bats migrate seasonally from many summer colonies to a smaller number of swarming caves?

This study shows that bats migrate from many summer roosts to the same cluster of swarming caves. Several studies have shown bats travelling from summer roosts in a large catchment area to a smaller number of caves to hibernate (e.g. Griffin, 1970; Tuttle, 1976), but few studies have shown bats migrating from several summer roosts to swarm together. Recaptures of two Myotis myotis were made between a swarming cave and two summer roosts by Bauerová and Zima (1988) and Parsons and Jones (2003) recaptured one female Natterer’s bat from each of three nursery roosts at one swarming cave.

Swarming, and hence mating, of bats from many summer colonies may be an important source of gene flow between otherwise dispersed summer colonies. Higher genetic diversity at swarming sites (Kerth et al., 2003; Veith et al., 2004) supports the idea that bats from several summer colonies are present at the same swarming site but does not necessarily show that they are mating there. Genetic analysis on Natterer’s bats from the current study (Rivers et al., 2005) provides evidence that most or all of the mating does occur at the swarming sites.

4.9. Are both sexes of Natterer’s bats philopatric?

Natterer’s bats ringed at summer roosts were never recaptured at a different summer roost. Smith (2000) also found no movements between Natterer’s bat summer colonies, even when only 2.6 km apart. Červený and Horáček (1981) found the occasional recapture of ringed Natterer’s bat in other summer colonies, but they did not publish further details.

The analysis of the Wareham bat box data provides evidence that both sexes are highly philopatric and that dispersal away from the natal area is low. Not all bats were recaptured, but this is to be expected for several reasons. Some bats die, with mortality especially high in the early years (Funakoshi, 1991). The bat boxes probably represent just a small proportion of each bat’s pool of roosts, so the probability of catching a bat on a given occasion in a bat box will be low. Furthermore, the often solitary roosting habits of males make them less likely to be caught. It is possible that some bats disperse outside of the study site but this seems unlikely to be a significant occurrence, or we would expect to recapture at least some bats in other bat boxes in the study area as they dispersed. A study of a subspecies of Natterer’s, M. nattereri bombinusi, supports the idea that juvenile and adult females are faithful to their summer roosts (Funakoshi, 1991).

Philopatry in both males and females seems to be rare in bats (Bradbury and Vehrencamp, 1977; Castella et al., 2001; Petit et al., 2001; Kerth et al., 2002). One example where it has been shown is in the swarming species P. auritus. Adults of both sexes show high fidelity to summer roosts and some individuals ringed as juveniles were recaptured at their natal site (Entwistle et al., 2000). However, the recovery rates for juveniles were low (females 22/71, 31%, males 10/52, 19%).

The lack of dispersal in philopatric species has important implications for gene flow. It is important for these bats to mate somewhere other than their summer roost to avoid inbreeding. Veith et al. (2004) suggest that swarming sites serve as mating sites to allow gene flow in P. auritus and we suggest this is also the case in M. nattereri.

4.10. How many bats swarm at the Windy Pits?

We estimate that 300–400 bats visit each Windy Pit per night during the swarming season and that the three main Ryedale Windy Pits support a population of approximately 5000 bats, of which approximately 4000 are Natterer’s bats. The published population estimate for Natterer’s bats in England is 70,000 (Hutson, 1993). Our estimate suggests either that these caves support a significant proportion of the English population or that the national population has been underestimated. Either way, this has significant conservation implications, as the UK population of Natterer’s bats may be of international importance and therefore deserves special attention (Stebbings, 1988; Hutson, 1993). The Windy Pits are clearly important, probably both as swarming and hibernation sites, as they support a large number of bats from a large catchment area, possibly due to the rarity of suitable underground sites in the area.

4.11. Which methods can be used to measure bat swarming activity?

The logging, catching and observation methods provide different measures of bat activity. Employing all three methods allowed us to estimate how these measures relate to the estimated number of bats swarming each night. Our estimates suggest that automatic logging and video/nightscope observations overestimate the number of bats present about three to fourfold, and that we catch about 10% of the bats present. The proportion caught will depend on trap efficiency.

4.12. Why conduct autumn surveys as an alternative to winter surveys?

An English Nature database of 991 bat hibernacula highlights the difficulty of surveying crevice-dwelling species. Only 325 had more than 10 bats recorded, only 42 had over 100 bats, and only four over 400 bats (Altringham, 2003). Very few species were recorded in each cave, mostly bats in the genus Rhinolophus which tend to hang from the ceiling. Only 10 sites with over 100 bats were dominated by bats in the genus Myotis and none of these were caves (Altringham, 2003). The number of recorded hibernating bats is only a fraction of the population estimates for England, due to the difficulties of surveying underground sites, especially natural caves.
This study clearly shows that autumn surveys can provide more information on bat population sizes than winter surveys alone. Crevice-dwelling species, such as Natterer’s bats, are under-estimated by traditional winter survey methods (Hall and Brenner, 1968; Stebbings, 1988; Degn et al., 1995; Parsons et al., 2002). Autumn surveys also cause less disturbance than hibernation surveys which may lead to arousal of bats and the depletion of limited energy reserves (Thomas, 1995). Although autumn capture at cave entrance can also cause disturbance, it does not involve arousal of torpid bats, and there are non-invasive alternatives (Degn et al., 1995; Parsons et al., 2003).

4.13. What role does protecting swarming sites play in bat conservation?

Natterer’s bats and many other temperate bat species use several roosts through the year and roost availability may be a limiting factor for bat populations (Racey and Entwistle, 2003). Therefore conservation must consider year-round roost requirements and include sites used for mating, as well as hibernation, nursery and general roosting sites. Underground sites supporting large swarming and/or hibernating populations should be given special protection. This study shows that bats often return to the same swarming site, therefore populations may suffer if a cave is made unsuitable for swarming by disturbance, microclimate change or entrance closure to prevent human access (Stebblings, 1988; Pierson, 1998). One solution is to use bat gates that allow access to bats but not humans, though gates need to be carefully designed so as not to interfere with swarming behaviour (Pugh and Altringham, submitted for publication).

For species that migrate seasonally, requirements are more complex and conservation requires larger-scale plans and co-operation (Myers et al., 1987; Pierson, 1998; Fleming and Eby, 2003). Racey and Entwistle (2003) suggest that an effective management unit for bats should be the colony and its main roost and peripheral and seasonal roosting sites, along with surrounding foraging areas and connective elements. We suggest that mating sites should be specifically included in the management unit. The structure of the landscape and its mosaic of habitats will determine not only summer commuting patterns, but on a larger scale, patterns of seasonal migration. A combination of landscape ecology and population genetics will give a more complete picture and better inform conservation policy. ‘Migratory connectivity’ of the year-round habitats required by bats needs to be considered, as it is for birds (Webster et al., 2002).

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