

Winter activity of a population of greater horseshoe bats (*Rhinolophus ferrumequinum*)

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Abstract

Activity patterns of greater horseshoe bats *Rhinolophus ferrumequinum* were investigated at caves in Cheddar (south-west England) during the hibernation season. An ultrasound detector and datalogger were used to monitor and record the number of echolocation calls in a single cave. Activity of *R. ferrumequinum* remained largely nocturnal throughout winter, and the mean time of activity over 24 h was 88 to 369 min after sunset. There was an increase in diurnal activity from late May to early June, probably because bats remained active after foraging at dawn towards the end of the hibernation season. Visits to the cave did not increase bat activity. Cave air temperature reflected external climatic temperature, although there was variation in cave temperature and its range within and among caves. Individual *R. ferrumequinum* are usually dispersed in caves in regions where temperature fluctuations correlate with climatic variations in temperature. There was a positive correlation between the number of daily bat passes monitored by the bat detector and datalogger (= daily activity) and cave temperature. Nocturnal activity may be sometimes associated with winter feeding. Neither date nor barometric pressure had a significant effect on daily activity. Activity patterns largely reflected the findings from individual *R. ferrumequinum* studied by telemetry (Park, 1998), in that bat activity increased with cave and climatic temperatures, and the temporal pattern of activity remained consistently nocturnal throughout winter, starting at dusk.

Key words: hibernation, torpor, Chiroptera, activity patterns, *Rhinolophus ferrumequinum*

INTRODUCTION

Population studies of bat activity

Many workers investigating bat activity examine activity levels of populations of bats, and do not observe the behaviour of individuals directly. Results from these studies are often then used to make deductions about individual behaviour (e.g. Thomas, 1993).

Ultrasound detectors are often used for assessing bat activity, and broad-band detectors can be used to discriminate between some species (Vaughan, Jones & Harris, 1997). Simple narrow-band detectors tuned to a single frequency can be used to identify species if only one species echolocates at a given frequency in a particular area (e.g. Nagel & Nagel, 1997). Alternatively, population estimates of species in hibernacula may enable the investigator to ascertain which species accounts for the majority of data collected (e.g. Thomas,

1993). If activity patterns differ among species, however, it would be difficult to make inferences about the behaviour of any particular species.

Infra-red light barriers positioned in hibernacula can detect the flight activity of bats during arousals from torpor (Nagel & Nagel, 1994; Thomas, 1995). Using a photo-electric beam-splitter to trigger a camera and flash, photographs of bats inside caves and mines can be taken. Not only does this technique allow discrimination between those bats leaving and those entering the cave but it may also allow species identification (Daan, 1970, 1973; Lubczyk & Nagel, 1995).

Bat activity during the hibernation period

Throughout this paper the hibernation terminology used follows that given by Ransome (1990). Bat activity reaches its lowest levels during mid-winter when the proportion of time spent in torpor is greatest (Daan, 1973; Nagel & Nagel, 1994, 1997; Degn, Andersen & Baagøe, 1995; Lubczyk & Nagel, 1995; Thomas, 1995). Ransome (1968, 1971) showed that *R. ferrumequinum*

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selects lower cave temperatures at this time, and arouses least often. He also produced indirect evidence for successful foraging throughout the hibernation period, whenever external air temperature exceeded 10°C and permitted insect flight (Ransome, 1968, 1971). Foraging is the only post-arousal activity in winter which requires arousal to be synchronized with dusk. Dusk is the most favourable time for foraging, since darkness permits flight outside the hibernaculum at a time of highest external air temperatures than during any other period of the night. If successful, foraging leads to prolonged nocturnal activity while food is digested.

Studies have produced conflicting data on the extent to which bat activity remains nocturnal during winter. In a population consisting largely of *Myotis daubentonii*, less activity occurred during the day than at night throughout winter (Daan, 1973). The pronounced nocturnality, however, that characterizes activity patterns in October diminishes as the season progresses, before increasing again in late winter (Daan, 1973; Nagel & Nagel, 1994). Diurnal activity increased in a hibernaculum containing *M. daubentonii* and *M. nattereri* from 2.4% in October to 8.7% in December (Lubczyk & Nagel, 1995). It is not clear if this result is statistically significant, however, and activity is still very much biased towards nocturnality in December. Thomas (1995) studying *Myotis lucifugus* and *M. septentrionalis* activity between January and March found no difference in the number of day and night-time flights which were detected by an infra-red beam. During April there was an increase in the proportion of night-time flights. This contrasts with a study using an ultrasound detector to monitor bats at the same site, which found consistently more activity at night than in the day over the winter (Thomas, 1993). Most activity of *Rhinolophus hipposideros* registered by ultrasound detectors occurred between sunset and sunrise throughout winter (Nagel & Nagel, 1997). These conflicting results may reflect species and locality differences in the potential for winter foraging, which must be influenced by the severity of the local winter climate, and insect availability.

Studies of population activity that use the methods described above can accumulate considerable data over long time periods. Because the systems are automated they are less time-consuming than, for example, radio-telemetry studies of individual bats. Most importantly, they involve minimal disturbance. Few studies, however, are able to ascertain to what extent the behaviour of a population reflects individual behaviour. In another study (Park, 1998) the thermoregulatory activity patterns and flight behaviour of individual *R. ferrumequinum* over the hibernation season were determined by using temperature-sensitive radio-transmitters. The aim of this study was to describe the activity of a hibernating population of bats in a cave, and to compare these results with those from a radio-telemetry study carried out concurrently. This comparison should determine the validity of inferring individual behaviour from population behaviour.

METHODS AND MATERIALS

The study was carried out during the winters of 1995/6 and 1996/7, in Gough's Old Cave in Cheddar Gorge (south-west England: Ordnance Survey Grid reference ST468539). This is the main bat hibernaculum in Cheddar Gorge, and is *c.* 75 m long and 20 m deep (Barrington, 1964). Approximately 20 m inside this cave is an opening to the entrance of Long Hole, a 255 m passage above Gough's Old Cave. *Rhinolophus ferrumequinum* also sometimes hibernates in two other caves in the Gorge, Canyon Cave and Whitespot which are 45 m and 55 m long, respectively (Ransome, 1968).

Echolocation calls of *R. ferrumequinum* were monitored and used as a measure of activity. *R. ferrumequinum* emits constant frequency calls at around 83 kHz (Jones & Rayner, 1989). An ultrasound detector (Mini-2; Ultra Sound Advice, London, UK), with a bandwidth of ± 4 kHz, was tuned to 83 kHz and each call detected was converted to a 36 ms voltage pulse (square wave) by a Schmitt trigger (custom-built by L. Teagle). The device was not triggered by ultrasound pulses (produced by a GTI ultrasound generator; QMC Instruments, London, UK) similar to those emitted by other echolocating bat species in the area, including *R. hipposideros*, the most common other species hibernating in the caves. *Rhinolophus hipposideros* emits calls at 109–117 kHz (Jones, Gordon & Nightingale, 1992). The ultrasound detector and Schmitt trigger were powered by a 6 V 10 Ah motorcycle battery. A datalogger (Series 800 8-bit Squirrel logger; Grant Instruments, Cambridge, UK) registered the total number of square waves received from the trigger every 10 min. A temperature probe (accurate to 0.2°C) was attached to the datalogger, and ambient cave temperature was averaged over 10 min intervals. This equipment was placed in a sealed plastic box with bags of silica gel to reduce humidity and positioned *c.* 20 m inside the cave from the main entrance (=middle site). Bats leaving and returning to the cave via the main entrance were detected by the ultrasound detector. Bats flying into the cave via a smaller second entrance may not have been detected until they reached their preferred hibernation sites. This second entrance, however, has a horizontal grille with narrow bars protecting it, and it is much less likely to be used than the larger vertical grille with wider spaces, at the main entrance.

The number of echolocation call counts per 10 min period (referred to as activity in future) and temperature records stored in the datalogger were downloaded onto a laptop computer every 7–10 days during visits to the cave. Approximately 5 visits a month were made to Gough's Old Cave from late October to late May or June during the winters of 1995/6 and 1996/7. Each visit lasted an average of 50 min (range 5–110 minutes) but the time spent within the main part of the cave was only about 15 min, as the data were downloaded by the main entrance, away from the bats. On most visits only one person entered the cave and lights were kept away from the walls and ceilings where the bats were roosting. In

this way disturbance was minimized. The bats were, however, disturbed and handled during 3 daytime surveys carried out every winter in October, January and April. Any data collected within the 24 h period after these surveys were omitted from activity analyses. The distribution of *R. ferrumequinum* throughout the cave during the study, except on the day of these surveys, was unknown.

The hibernation season was divided into 4 winter periods; early winter (mid-October to mid-December), mid-winter (mid-December to mid-February) late winter (mid-February to mid-April) and spring (mid-April to late May). In 1996/7 data were collected until 6 June 1997. All times referred to throughout this study are Greenwich Mean Time.

Temporal distribution of activity

Activity data were plotted against time of day, and mean daily activity within each 10 min interval was calculated for each winter period in both 1995/6 and 1996/7. For each winter period, Rayleigh's test for randomness was used to determine whether there was a bias in the time distribution of activity (Batschelet, 1981). Absolute time was used for this circular statistical analysis, not time relative to sunset. Sunset times within each winter period varied by only 50–100 min, representing angles of 12.5–25° which are sufficiently narrow for any bias towards arousing at sunset to be detected. The time that each echolocation call was recorded was converted to degrees and the mean direction and length of the mean vector (r) for each winter period calculated. Mean direction represents the mean time of activity over 24 h within each winter period. Mean vector length is a measure of the concentration of data around the mean, ranging from 0 to 1 with increasing concentration. For large sample sizes z is used as the test statistic for Rayleigh's test. This is calculated by $z = nr^2$ where n represents the sample size (Batschelet, 1981).

Disturbance

In order to ascertain whether bats were disturbed by visits to the cave, we compared the amount of activity occurring between the end of a cave visit and sunset time with the amount of activity occurring during the same time period on the previous day. No unauthorized entrance to the cave was possible as both entrances were grilled.

Cave temperatures

Ambient cave temperature (accurate to 0.2°C) was also monitored by the main entrance (= front) and *c.* 30 m inside the cave, from the main entrance (= back) using 2 temperature probes (Tinytalk; Orion Components,

Chichester, UK). Temperature probes were positioned at similar heights (1–2 m) throughout Gough's Old Cave to minimize any possible effect of a height-dependent temperature gradient. Each temperature probe was programmed to take a reading every 72 min, and data were downloaded every 3 months. Another temperature probe was positioned at a height of 2 m about 20 m inside Canyon Cave (length *c.* 45 m), close to where the bats roosted. Canyon Cave is another cave with dynamic air-flow, and most bats that hibernate there roost at 3–4 m height. Climatic temperature (accurate to 0.1°C) was measured at sunset each night outside Gough's Old Cave and Canyon Cave by using a digital thermometer. Sunset was ascertained by using Whitaker's Almanac (Marsden, 1995–1997). The relationship between cave temperature (at the front, middle and back of Gough's Old Cave and from Canyon Cave) and climatic temperature close to sunset was determined using linear regression analysis.

Barometric pressure

Daily barometric pressure readings (mb) were obtained from The Meteorological Office (Bristol Weather Centre, *c.* 20 km north-east of Cheddar Gorge) for November 1995 to May 1996. Daily pressure readings taken around sunset were used and these were corrected to sea level measurements.

Activity levels throughout winter

The relationship between total daily activity and mean daily cave temperature (from the middle of Gough's Old Cave) was determined by using Spearman rank correlations as data could not be normalized. An analysis of covariance (ANCOVA) was used to investigate the effects of winter period (factor) and barometric pressure (covariate) on activity for the winter of 1995/6. The square roots of total daily activity data were used to achieve normality.

Comparison with individual bats

The amount of total daily activity was compared with the proportion of radio-tagged bats arousing each night (Park, 1998).

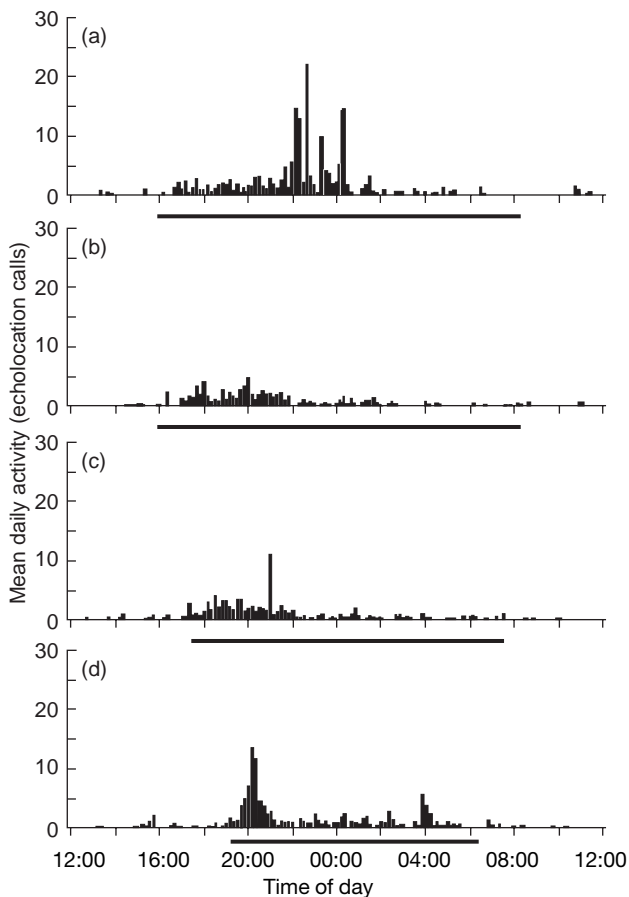
RESULTS

Population size

The total number of *R. ferrumequinum* found in Cheddar Gorge during each of the three surveys in the winters of 1995/6 and 1996/7 varied between 48 and 67 bats, with 8–65 bats frequenting Gough's Old Cave (Table 1).

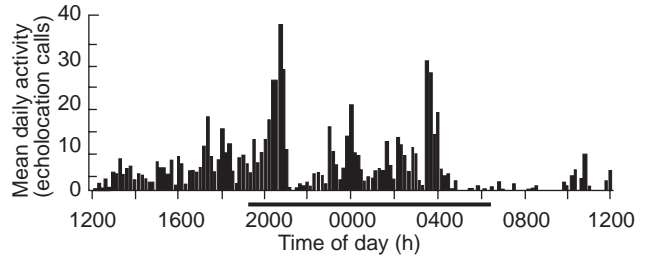
Table 1. The number of *R. ferrumequinum* found in Gough's Old Cave (including Long Hole), Canyon Cave and Whitespot

Date	Gough's Old Cave	Canyon	Whitespot	Total bats
28 October 1995	65	1	1	67
20 January 1996	8	53	1	62
6 April 1996	10	37	6	53
26 October 1996	52	14	0	66
18 January 1997	32	5	11	48
5 April 1997	28	24	2	54

**Fig. 1.** Temporal distribution of mean daily activity over a 24 h day during the winters of 1995/6 and 1996/7 combined. Each column represents a 10 min interval. (a) early winter, (b) mid-winter, (c) late winter, (d) spring (mid-April to late May). The black bars under the x-axis indicate the longest period between sunset and sunrise within each winter period.

Temporal distribution of activity

Most activity occurred between sunset and sunrise; only 12.7 % of activity took place during the day (Fig. 1). This nocturnal pattern was consistent throughout winter. During the spring period of 1997, when data were added from late May to 6 June, the temporal distribution of activity changed greatly (Fig. 2). A larger proportion (31.6 %) of the activity recorded took place

**Fig. 2.** Temporal distribution of mean daily activity over a 24 h day from mid-April to early June 1997. Each column represents a 10 min interval. The black bar under the x-axis indicates the longest period between sunset and sunrise over these dates.

during the day although the two main peaks of activity were at 21:00 and just before 04:00 (i.e. *c.* 1 h after sunset and 1 h before sunrise).

All winter periods showed a non-random temporal distribution of activity (Table 2). Mean time of activity varied from 19:46 to 22:26, a range of only 160 min. Changes in the mean time of activity did not appear to correspond to changes of sunset time.

Disturbance

There was no significant difference in the amount of activity occurring between the end of a cave visit and sunset time compared with the amount of activity occurring during the same time period on the previous day (Wilcoxon signed rank test $W_{48} = -26.0$, NS). The median amount of activity before a cave visit = 0.0 (interquartile range 0.0–2.5), and after a visit = 0.0 (0.0–1.5).

Cave temperatures

There was a significant positive relationship between climatic temperature and cave temperature at sunset throughout Gough's Old Cave and in Canyon Cave (linear regression for front, middle and back of Gough's Old Cave and Canyon Cave: $F_{(1,200)} = 753.3$, $P < 0.0001$; $F_{(1,130)} = 357.1$, $P < 0.0001$; $F_{(1,134)} = 127.7$, $P < 0.0001$; $F_{(1,110)} = 66.4$, $P < 0.0001$, respectively). All the regressions were highly significant although the percentage of variation in cave temperature that is due to variation in climatic temperature (r^2) was higher at the front and in the middle of Gough's Old Cave than at the back, and in Canyon Cave where temperatures are more stable (Table 3). Cave temperatures from the middle of Gough's Old Cave are shown in Fig. 3.

On average, over the entire winter, the front of Gough's Old Cave was significantly colder and more variable than the back of Gough's Old Cave or Canyon Cave in the winter of 1995/6 and 1996/7 (1996/7: Post-hoc test Dunn's Method $Q = 40.5$, $P < 0.05$; $Q = 18.3$,

Table 2. Results of Rayleigh's test for randomness on activity times for each winter period during the winters of 1995/6 and 1996/7. Mean time of activity and sunset time within each winter period are given, z = test statistic, n = total number of echolocation calls recorded. Spring (to late May) 1997 includes activity recorded from mid-April to late May (see Fig. 1d). Spring (to early June) 1997 includes activity recorded from mid-April to early June (see Fig. 2)

Winter period	Mean time of activity	Mean sunset time	Mean vector length (r)	z	P	n
Winter 1995/6:						
Early winter	21:15	16:17	0.65	33:10	< 0.0001	7834
Mid-winter	19:46	16:37	0.68	25:23	< 0.0001	5457
Late winter	20:02	18:22	0.71	28:68	< 0.0001	5689
Spring	21:35	19:41	0.74	22:54	< 0.0001	4117
Winter 1996/7:						
Early winter	22:26	16:17	0.87	51:07	< 0.0001	6747
Mid-winter	20:50	16:37	0.69	15:37	< 0.0001	3229
Late winter	21:10	18:22	0.74	25:92	< 0.0001	4733
Spring (to late May)	22:16	19:41	0.54	59:90	< 0.0001	4378
Spring (to early June)	21:20	19:52	0.41	12:76	< 0.0001	35636

Table 3. Median cave temperatures and inter-quartile ranges (25% and 75%) for the front and back of Gough's Old Cave and for Canyon Cave. Temperatures for Canyon Cave during the winter of 1995/6 were only monitored from January 1996 and are not included in this table. n = number of temperature recordings

Winter	Median temperature (25%–75%)	n	Test
1995/6:			
Front Gough's Old Cave	4.9 (3.0–7.5)	2738	Mann–Whitney $T = 5513573$
Back Gough's Old Cave	7.5 (7.2–9.0)	3137	$P < 0.0001$
1996/7:			
Front Gough's Old Cave	6.0 (3.7–7.9)	3208	Kruskal–Wallis $H = 1647$
Back Gough's Old Cave	8.2 (7.2–8.6)	3208	$P < 0.0001$
Canyon Cave	7.2 (6.0–7.9)	3208	

$P < 0.05$ respectively; Table 3). The back of Gough's Old Cave and Canyon Cave both had fairly stable temperature regimes, but Canyon Cave was on average, 1 °C colder than the back of Gough's Old Cave during the winter of 1996/7 ($Q = 22.2$, $P < 0.05$).

Activity levels throughout winter

During both winters, total activity recorded each day was generally under 400 calls although occasionally high levels of activity were recorded for 1 or 2 days. The amount of activity recorded between late May and early June 1997 was very high (Fig. 3b).

During both winters there was a positive correlation between daily activity and cave temperature over the period between late October and May/June (Spearman rank correlation coefficient $r_{s,188} = 0.15$, $P < 0.05$; $r_{s,203} = 0.30$, $P < 0.001$ for 1995/6 and 1996/7, respectively). The coefficient for these correlations, however, was low. Figure 4 shows that low activity levels could occur whatever the cave temperature, but high levels occurred only at relatively high cave temperatures.

Data from each year were split into separate winter periods in an attempt to control for non-temperature-dependent seasonal effects. Only in spring 1997 did daily activity increase with an increase in cave temperature ($r = 0.72$, $P < 0.001$, $n = 48$). Cave temperatures

(from the middle of Gough's Old Cave) were significantly higher in spring 1997 than in spring 1996 (Mann–Whitney $_{48,34} T = 908.5$, $P < 0.0001$).

Overall, cave temperature and daily activity were positively correlated but, with the exception of the warm spring in 1997, there was no correlation between cave temperature and daily activity within each winter period, and little difference between winter periods.

In the ANCOVA to analyse the effect of winter period and barometric pressure on activity, the interaction term between winter period and barometric pressure was not significant so was removed from the model and the ANCOVA repeated. There was no effect of winter period or barometric pressure on the square roots of daily activity of *R. ferrumequinum* (winter period $F_{(3,183)} = 2.06$, NS; barometric pressure $F_{(1,183)} = 2.42$, NS).

Comparison with individual bats

There was a positive correlation between the total daily activity of the population of *R. ferrumequinum* recorded in this study and the proportion of radio-tagged individuals that aroused each night (Park, 1998) (Spearman rank correlation coefficient $r_{s,(215)} = 0.15$, $P < 0.05$).

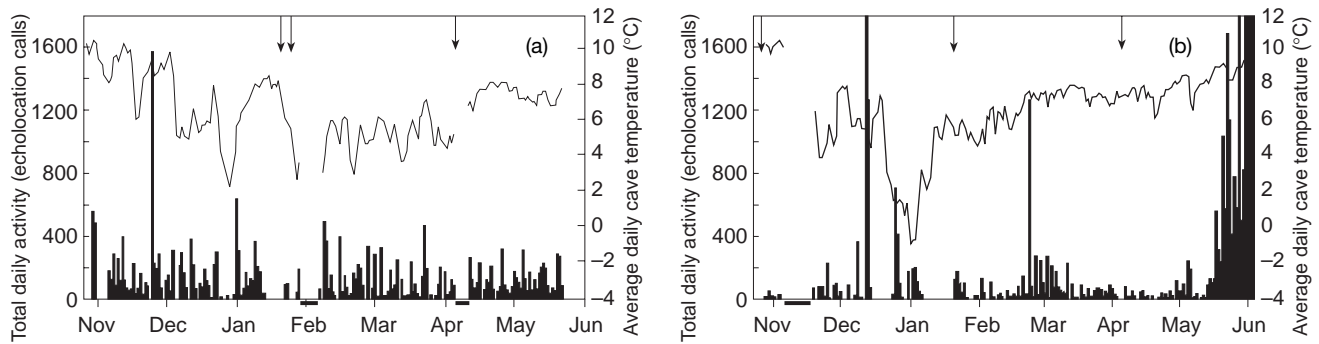


Fig. 3. Total daily activity (bars) and average daily cave temperature (lines) from (a) November to late May during the winter of 1995/6, and (b) November to early June during the winter of 1996/7. Each activity bar represents a day. Arrows indicate the date of surveys in October, January and April each winter. In the winter of 1995/6 bats were disturbed twice in January for radio-tagging. Data from these days and the subsequent 24 h have been omitted. The black bars under the x-axis represent periods of time when no data were collected due to equipment failure.

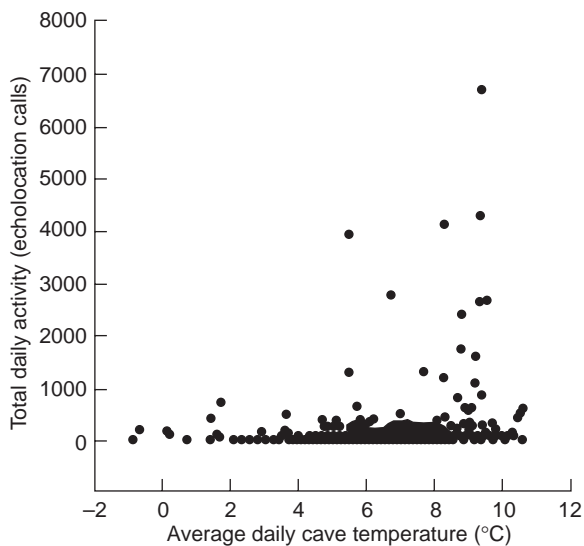


Fig. 4. The relationship between total daily activity and average daily cave temperature. Data from 2 years were combined.

DISCUSSION

The amount of activity recorded by an ultrasound datalogger at a particular location in a specific cave will potentially be influenced by many variables. These include the number of bats present, their arousal frequency, the duration of their post-arousal activity and the entry of active bats from other caves. In addition, the position and sensitivity of the bat detector will influence how much activity is recorded. The system used here probably detected bats over about 10 m, and was located in a position which monitored all bats exiting, and most entering the study cave. It could not record calls from bats that had left to forage outside the cave, or those which may have clustered in high rifts beyond the range of the bat detector, after foraging. Hence the activity levels must be regarded as minima.

Temporal distribution of activity

The activity of greater horseshoe bats remained nocturnal throughout winter, with the mean time over 24 h from 88 to 369 min after sunset. The average arousal duration of radiotagged *R. ferrumequinum* in winter was 260 min, but ranged from 37 min to 54 h 24 min (Park, 1998). Hence the variability of arousal duration among individuals accounts for some of the changes in mean activity time, and explains why changes in activity times do not correspond precisely with changes in sunset time.

Thomas (1993) found that, although there was more activity of myotis bats (*Myotis lucifugus* and *Myotis septentrionalis*) at night than in the day, there was little concentration around any one time. A laboratory study of the big brown bat *Eptesicus fuscus* showed that individuals aroused for *c.* 90 min (Twente & Twente, 1987), so Thomas (1993) predicted that if arousals occurred at dusk, the spread of activity throughout the night would be minimal. Post-arousal activity durations obtained in laboratory studies, however, should be treated with caution, as conditions in the laboratory do not reflect those in the field, and the bats in these studies were unable to fly after arousals as they do in the wild. In addition to this, activity durations of *E. fuscus* may differ from those of *M. lucifugus* and *M. septentrionalis*. Thomas (1993) suggested that arousal time becomes random when bats lose 'zeitgebers' (synchronizing factors) in winter. The present study shows that this does not happen in *R. ferrumequinum*. This may be because either daily external temperature fluctuations, and/or their frequent arousals followed by occasional foraging success, permit synchronization of their biological clocks with dusk. Griffin & Welsh (1937) showed that the arousal rhythm of bats could be entrained by feeding.

There was an increase in diurnal activity from late May to early June as bats spent less time in torpor towards the end of the hibernation season. This

probably occurs due to the increasingly regular occurrence of successful foraging at dawn. Time-lapse video recordings show that most mid-winter foraging occurs around dusk, but as external temperature rises in spring, dawn foraging starts (R. D. Ransome, pers. obs.). Any successful foraging bout requires an extended period of thermoregulatory activity whilst food is being digested and the bulk of the faeces egested. This can take from 6 to 12 h in *R. ferrumequinum* (Ransome, 1978) but may be much shorter in other species.

If only dusk foraging occurs, *R. ferrumequinum* activity is predicted to be entirely nocturnal. If both dusk and dawn foraging is successful, activity may last for 24 h of the day, and for several days continuously in mild spells. While this thermoregulatory activity is happening, bats tend to cluster together in a suitable vertical rift where they can build up a warm microclimate for economical digestion. This behaviour leads to accumulations of faecal pellets at any time of the winter in temperate climates (Ransome, 1968). In the very mild weather in February 1998 faecal dry mass levels per bat per day at a maternity site in Gloucestershire exceeded those typical of May (R. D. Ransome, pers. obs.).

Other studies, in which activity periods were found to be more or less random in mid-winter (Daan, 1973; Thomas, 1995), show an increasing nocturnal tendency in late winter and early spring. However, these studies did not continue until May. Differences among studies may be explained by the onset of dusk foraging in spring following an absence of mid-winter foraging under severe continental climates, and bats leaving the hibernacula for other roosts as soon as dawn foraging begins.

Disturbance

Laboratory studies of torpid vespertilionid bats suggest that they do not arouse in response to non-tactile stimulation such as light, sound and small temperature fluctuations (Speakman, Webb & Racey, 1991). In contrast, Thomas (1995) studying a natural population of two *Myotis* species, provided evidence that non-tactile disturbance did provoke arousals. We found no evidence of increased activity after visits to Gough's Old Cave. The *Myotis* bats in Thomas's study (1995) were found at much higher densities than the bats in ours, and in close contact. Since these *Myotis* bats aroused at random times in winter (Thomas, 1993), some bats would always have been close to their arousal time, whatever time the mine was visited. If these bats were provoked to arouse, they may have disturbed others in a 'cascade' effect as they left their group. In addition, it should be stressed that we attempted to minimize the disturbance to the bats in this study whereas Thomas (1995) was specifically investigating the effects of non-tactile stimulation, so the bats in his study may have been subjected to higher levels of disturbance.

Cave temperatures

Cave temperature in this study strongly reflected external (climatic) temperature. Gough's Old Cave and Canyon Cave are the main hibernacula used by bats in Cheddar Gorge, hence most bats roosting in the open in these caves could almost certainly detect climatic temperature changes from fluctuations in air temperature at their roosting position. Bats that roost further underground in large cave systems, where the air temperature is virtually constant, are not able to do this (e.g. Paige, 1995).

The temperature regimes within different parts of the cave, however, differed. At the front of Gough's Old Cave, air temperature was on average 2.2–2.6 °C lower and fluctuated far more than at the back of Gough's Old Cave and Canyon Cave which had more stable temperature regimes. Bats often form clusters in Canyon Cave during cold weather but move near the entrances of Gough's Old and Long Hole Caves when external temperature increases, perhaps to evaluate feeding conditions better (R. D. Ransome, pers. obs.). *R. ferrumequinum* prefers the more stable temperature regime of Canyon Cave when conditions for feeding are poor (Ransome, 1968: Gough's Old = Cave C; Canyon Cave = Cave E, and Whitespot = Cave G). Individuals of this species are rarely found at the back of Gough's Old Cave which has a similarly stable temperature regime but was, on average, 1 °C warmer than Canyon Cave. Most of the cave temperatures reported here fall within the range of temperatures (3.0–13.0 °C) at which *R. ferrumequinum* has been recorded torpid in other hibernacula (Ransome, 1968, 1971; Webb, Speakman & Racey, 1996).

Activity throughout winter

In this study there was no marked reduction of activity as winter progressed, although recordings did not begin until the end of October and activity may have been higher earlier in the month. Activity of *Rhinolophus hipposideros* within hibernacula was found to increase at the end of winter, during April and May (Nagel & Nagel, 1997). An increase in activity during these months was not observed in the cold spring of 1996 in this study. However, activity increased in late May and early June in 1997, when temperatures were warm. Ransome (1971) showed that *R. ferrumequinum* can hibernate until the end of May, later than is usually reported for temperate bats at similar latitudes. His findings are confirmed by observation of radio-tagged bats that remained in torpor for up to 6 days continuously during late May (Park, 1998).

Overall, there was a positive correlation between daily activity level and cave temperature each winter, but this was primarily due to the influence of activity records from mid-April 1997 onwards. Cave temperatures were

significantly higher in 1997 than in 1996 during this period. This suggests that activity only relates to cave temperature during warm spring weather conditions. Arousal frequency of *R. ferrumequinum* increases with an increase in climatic temperature, but the duration of post-arousal activity is largely unaffected until climatic temperatures reach 10 °C or above (Park, 1998). Since this is the temperature above which significant numbers of insects are likely to fly (Ransome, 1968; Rydell, 1989; Jones, Duvergé & Ransome, 1995), it suggests that the activity duration extension relates to foraging. However, below 10 °C activity still occurs after arousals, which is probably unrelated to foraging.

Cave air temperature does not influence winter flight activity in *Myotis myotis*, but activity increases with a reduction in barometric pressure (Nagel & Nagel, 1994). In this study, the amount of daily activity was not related either to cave temperature in most winter periods or to barometric pressure.

Activity patterns in populations of hibernating bats

The activity behaviour of bats during the hibernation season will be partly determined by the species of bat and the climatic conditions to which individuals are exposed. For example, *M. lucifugus* roosting in hibernacula in Canada during winter is less likely to be able to forage successfully after arousing than *R. ferrumequinum* in Britain due to the severity of Canadian winters and the lack of available insects (D.W. Thomas, pers. comm.). There seems to be little adaptive function in synchronizing arousals with dusk in bats when insects are scarce or absent.

Random diurnal activity patterns suggest that a free-running state operates, and imply therefore that foraging is not cost-effective. Activity starting at dusk, as we have shown, indicates that foraging at dusk is frequently successful enough for arousal to be synchronized by a 'zeitgeber' such as daily cave temperature fluctuations. No other suggested activities during post-arousal thermoregulation require a bat to arouse at dusk. Bats can drink, excrete, mate or sleep at any time of the 24 h period.

This is one of the first studies to ascertain the extent to which the activity of a bat population reflects individual activity patterns. Total daily activity was positively correlated with the proportion of radio-tagged bats arousing each night (Park, 1998), and the temporal activity patterns found in this study reflected the findings from individual *R. ferrumequinum* (Park, 1998). Population studies investigating bat activity patterns usually involve less disturbance than those following individuals, and provided the limitations of such methods are recognized, they can be used to make some inferences about bat hibernation behaviour.

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