Activity patterns of insectivorous bats and birds in northern Scandinavia (69° N), during continuous midsummer daylight

J. R. Speakman, J. Rydell, P. I. Webb, J. P. Hayes, G. C. Hays, I. A. R. Hulbert and R. M. McDevitt

Previous studies suggest that many species of insectivorous bats are nocturnal, despite the relatively low availability of their insect prey at night, because of the risk of predation by diurnal predatory birds. We hypothesised that if this was the case bats living above the arctic circle would alter their feeding behaviour during midsummer because there would no longer be any benefit to restricting their activity to the period when their prey are least abundant. Alternatively, if bats were more influenced by competition from aerial insectivorous birds they would continue to feed at 'night' to avoid such competition. In northern Norway (69° N), during continuous midsummer daylight, insectivorous sand martins (*Riparia riparia*) concentrated their aerial feeding activity when aerial insects were most abundant. The birds stopped feeding between 23:00 and 07:00 when aerial insects were least abundant. In contrast, northern bats (*Eptesicus nilssonii*), fed mostly between 22:00 and 02:00, coinciding with the lowest aerial insect availability, and with the period when light levels were lowest (ca 1000 lux). Bat activity patterns were closest to those predicted by the avian competition hypothesis. The low densities of both sand martins and Northern bats in the study area, however, were less consistent with this hypothesis. Possibly populations of both species were higher historically and the observed patterns reflected historical competition. Bat activity was most closely correlated to ambient light levels. This raised two alternative explanations that we could not eliminate. Perhaps there was differential predation risk, between the brightest and darkest parts of the day, because the visual capacities of falcons are strongly dependent on luminance. Alternatively the bats may have been entrained to emerge at given light levels by their behaviour at other times of year.

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Throughout the world, independent of their diverse ecology and diets, the vast majority of bat species fly and feed almost exclusively during periods of darkness (Speakman 1995). For insectivorous bats, this activity pattern occurs despite the fact that, at least in the north temperate regions, aerial insect densities are greatest during the day (Williams 1961, Rydell 1992, Speakman 1995, Rydell et al. 1996). Moreover, in the north temperate regions, the short night may place constraints on the amount of energy that can be collected and ulti-

mately allocated to reproductive output (Speakman and Racey 1987, Kurta et al. 1989). Reproductive rates of insectivorous bats are uniformly low (Kurta and Kunz 1987) when compared with aerial insectivorous birds, which occupy the equivalent diurnal niche (Speakman 1995), suggesting that the restriction of activity to night may impose constraints on the reproduction of bats, perhaps via the available energy. Nocturnal insectivorous caprimulgiform birds also have low reproductive rates consistent with this hypothesis (Csada and

Brigham 1994) (but see Barclay 1994 for an alternative interpretation of low reproductive rates of bats and some birds based on calcium limitation).

Attempts to explain chiropteran nocturnality have focused on three potential disadvantages of flying during the day, which might offset the potential energetic advantages of daytime foraging. First, diurnal aerial insectivorous birds may out-compete bats, forcing them to feed at night. Although birds evolved in the late Jurassic about 95 million years before bats evolved in the Eocene (Jepsen 1970, Padian 1987, Feduccia 1995), by the late Eocene the insectivorous bats had diversified and were already nocturnal, long before the modern temperate diurnal aerial insectivorous birds (hirundines and swifts) evolved (Rydell and Speakman 1995). Consequently, competition was unlikely to have been a potent selective force for nocturnality in the early history of the insectivorous bats. Nevertheless, as insectivorous birds have proliferated in the diurnal niches, contemporary competition (e.g. Tugendhat 1966, Ollason et al. 1992) may prevent the expansion of insectivorous bats from their nocturnal niches.

Second, bats may be restricted to feeding at night because of the risks of predation by diurnal avian predators (Macy and Macy 1969, Gillette and Kimborough 1970, Shimmings 1985, Rowarth and Wright 1989, Speakman 1991a, 1995, Fenton et al. 1994, Speakman et al. 1994a, Rydell and Speakman 1995). Finally, high ambient daytime temperatures, combined with high levels of solar radiation, which is readily absorbed across the dark naked wing membranes of bats (Thomas and Suthers 1972, Thomas et al. 1991) may cause day flying bats to overheat. Bats flying in daylight may be more susceptible to hyperthermia than birds. Birds have highly insulated wings (Martineau and Larochelle 1988) which restricts the uptake of radiation, and they can dissipate the net endogenous and exogenous heat loads of flight via their unique respiratory system (Thomas et al. 1991) and unfeathered legs (Martineau and Larochelle 1988, Ward et al. in press). These latter mechanisms are unavailable to bats. A biophysical heat balance model (Speakman et al. 1994b, Speakman 1995) indicated that hyperthermia might indeed be a constraint for large (> 0.5 kg) bats between 40° N and S, but probably not for smaller bats at greater latitudes. Based on a survey of over 400 occurrences of daylight flying by bats in the UK (Speakman 1990, 1991a), outside the zone where hyperthermia might be important, it was concluded that predation risk was the major factor restricting expansion of bats into daylight in that area.

Along the west coast of Scandinavia, the warming influence of the Gulf stream presently makes it the only place on the planet where the 10°C July isotherm extends above 70° N (Fullard et al. 1983). The northern bat (*Eptesicus nilssonii*) occurs over much of Scandinavia to at least 70° N (Rydell et al. 1994), about 300 km beyond the arctic circle. At this latitude the sun is continuously above the horizon during midsummer, and for about 50 d there is no true night. There are at least seven species of raptorial birds common in the region, and several potential competitive aerial insectivorous birds (Bruun and Singer 1970, Haftorn 1971). Data concerning how bats react to the absence of darkness at high latitudes is of interest because it may shed further light on the evolution of chiropteran nocturnality. In particular if the risk of predation by diurnal birds is the most potent factor we predict bats would alter their activity to coincide with periods when insects are most abundant when in continuous light, because there would no longer be an advantage to foraging at 'night'. Alternatively if competition was the most important factor bats might remain constrained to feed in periods when their competitors are least active and their prey at low density. In the current paper we describe the diel activity patterns of the bats, insects, and insectivorous and raptorial birds during continuous summer daylight in northern Norway.

Methods

Study area

We made observations in the area known as the Innland, about 50 km east of the town of Bardu (69° N), between 7 and 16 July 1991. The study site included the sparsely populated valleys of Malselvdalen, Kirkesdalen and Dividalen, and the small villages of Holt and Overbygd. The valley bottoms, particularly around the villages, and in Malselvdalen and Kirkesdalen, consisted mostly of agricultural land. Within the area we located two extant bat roosts, one at Holt and one in Kirkesdalen, and a single colony of sand martins (*Riparia riparia*) in Malselvdalen. All records of flying bats and sand martins were in the immediate vicinity of the known colonies. Using ultrasound detectors and direct captures we identified both bat colonies as containing northern bats (*Eptesicus nilssonii*). The Kirkesdalen colony was a maternity roost and represents the most northerly record of reproductively active bats anywhere in the world (Rydell et al. 1994).

Activity monitoring

We recorded the activity cycles of bats, sand martins, other aerial insectivores, and raptors from 10 to 16 July, which represented about 12% of the total annual period without true night. We made 102 h of observations at the Kirkesdalen bat roost, 58 h at the Holt bat roost and 59 h at the sand martin colony.

Light and temperature

We measured light intensity using the light meters of SLR cameras. We used a reading of incident light taken

using standard 50-mm lenses pointing vertically upwards, with the camera settings at 100 ASA and a fixed aperture of f16. We recorded the shutter speed, and later calibrated the shutter speed readings with absolute measurements of incident light using a precision lightmeter (Gossen Mastersix). In identical conditions the three cameras gave the same readings. The calibration equation $\log_e$ lux $= 4.87 + 0.972 \log_e$ (1/shutter speed), had an r^2 of 0.98 ($n = 35$).

We measured air temperatures at the Holt and Kirkesdalen sites using thermistor probes linked to data loggers (Grant Instruments, Cambridge, Ltd). The probes were placed 1 and 2 m above the ground, and were permanently shaded by unheated buildings. At the sand martin colony we measured air temperatures using a mercury thermometer. For both light and temperature, we took readings approximately every half hour, but more frequently during the periods when there was emergence activity at the roosts.

Insects

We assessed the abundance of aerial insects by walking fixed routes in the vicinity of the Kirkesdalen and the Holt bat roosts, making 200 sweeps 1–3 m in the air with a circular insect net (radius 20 cm) attached to a 50-cm handle. At sites further south, northern bats generally feed around 10 m (Baagoe 1987, Rydell 1989). We do not know the heights at which northern bats fed in the study area, since we made few contacts with bats away from the colony. However, we expect that in the lighter conditions they would feed lower and closer to trees (Nyholm 1965, Rydell 1992) and therefore closer to the heights at which we sampled insects. Our limited encounters with feeding bats supported this assumption.

Insects were killed with a pyrethrum-based insecticide (Sybol) and placed in a white enamel tray where they were immediately divided into three size classes: (a) large (> 15 mm body length), (b) medium (10–15 mm body length), and (c) small (< 10 mm body length), and counted. We compared catches of insects, under similar environmental conditions (between 14 and 20°C) at each roost, across the different people operating the nets. One person consistently captured fewer insects than the other five observers (61% lower on average) between whom there were no differences. We excluded the observations made by this observer from the analyses.

We identified insects to order and measured the wing lengths (from attachment to body to tip of one wing) of 2300 insects collected at the Kirkesdalen roost. In a sub-sample of 275 insects, we also measured body length. There was a strong correlation between wing and body length ($r^2 = 0.976$, $n = 275$)

Sand martins

We observed the sand martin colony from about 50 m away, from a parked vehicle. We made a detailed drawing of the colony and recorded whether each hole was used or not. In this way we made a rough estimate of the minimum population of birds using the colony. The number of birds entering nest holes per 5-min period was recorded. At the end of each period we recorded the number of martins sitting on the telephone cables which ran along the road where we parked the vehicle. During our observations at the bat roosts and at the sand martin colony we recorded the occurrence of any raptorial birds and aerial insectivorous birds in flight.

To assess the reliability of our activity counts some simultaneous counts of activity were made by the three observers who worked at the colony (JRS, PIW and IARH). We simultaneously counted the numbers of birds entering nest holes in ten intervals of 5 min each and compared the data at the end of the entire test so that observers could not adjust their observations to match those of the other observers. There were strong correlations between the counts across all three observers. The average discrepancy was 1.5 emergence events ($n = 30$ comparisons, sd $= 1.2$). Since the mean event rate in the test runs was 18.4 per 5-min period, our test suggests that the mean error rate was about 8%.

Northern bats

We observed the numbers of bats which exited and entered each roost. The roost at Holt was a 30-yr-old two-storey wooden house. The roost at Kirkesdalen was a larger two-storey wooden building that had not been occupied by humans for about 20 yr. At the Holt roost the bats entered and exited from holes in the roofing felt around a chimney. At the Kirkesdalen roost they exited from two sites, one at a roof apex, and a second hole under the guttering on one side. It was possible at both the Holt and Kirkesdalen sites for one observer to continuously monitor all entrances and exits. However, during most observation sessions at least two observers monitored bat activity simultaneously.

Observations of bats were facilitated by operating an ultrasound bat detector continuously at both roosts (either a Pettersson D-980 or a Stag electronics Bat Box III). Although it was continuously light, the bats always used echolocation during their exits and entrances from the roosts and during the few encounters we had with bats away from the roosts (< 1 km away). At both roosts there was an asymmetry in the cover available to the bats which exited. We divided the potential exit directions into sectors which varied in the cover they provided (distance to trees) and recorded the directions in which bats left and returned to the roosts.

We collected samples of fresh droppings (probably deposited during the previous few days) from inside the Kirkesdalen roost after the activity observations had

ended. The nature of the Holt roost meant it was not possible to collect samples there. Insect remains in droppings were analysed following the methods described by Whitaker (1988). All faecal analysis was performed by JR who has extensive experience with this method for northern bats (Rydell 1989, 1992).

Analysis

We analysed the data in two ways. First, to reveal diel patterns in activity, or variation in environmental cues, we pooled the data across days, adjusting where necessary (for raptor observations) for differences in the sampling/trapping effort. These adjustments are made explicit in the Results section. To explore diurnal variation we divided the days into hourly (two-hourly for raptors as data were more sparse) intervals and assessed hour to hour variation using ANOVA. Second, we performed multiple regression analyses to explore the factors influencing the extent of activity of the different animal groups. For these analyses we did not pool the data across days but retained the use of hourly measurement periods as the sampling unit.

Results

Environmental variables

During the measurements (10–16 July) there was significant diurnal temporal variation in both the light intensity (Fig. 1a: ANOVA $F = 495.6$, $p < 0.001$, df $= 23,154$) and temperature (Fig. 1b: ANOVA $F = 318.7$, $p < 0.001$, df $= 23,154$). Light intensity reached a minimum around 01:00 (ca 1000 lux) which was on average about 1/70th of the light intensity at 12:00 (ca 70 000 lux). Mean light intensity was correlated ($r^2 = 0.9$ $p < 0.001$) with the predicted elevation of the sun above the horizon, which varied from a minimum of 2° to a maximum of 63° on 13 July (NASA satellite predictor software, Telonics Ltd.), the mid-day of the study period. Temperature reached a minimum around 02:00 and a maximum at around 10:00.

Insects

Counts of insects, per 200 sweeps, varied between 0 and 114. Across all catches the vast majority (> 98%) of these insects were small (< 10 mm wing length) dipterans. The majority of the remainder were lepidopterans, and there were occasional (< 0.05%) hymenopterans and coleopterans. The mean wing length of all measured insects was 5.6 mm (sd $= 2.4$, $n = 2300$).

We analysed the factors influencing total insect catches at each site (Kirkesdalen and Holt) separately. The catches at Kirkesdalen, were significantly but non-linearly related to temperature (Fig. 2). Light intensity,

and the interaction between light intensity and temperature were also significant independent predictor variables. The best fit least-squares equation was $\log_e[\text{Insect catch} + 1] = -2.91 + 0.459$ Temperature (°C) $+ 2.13$ Light intensity $- 0.152$ (Light intensity × Temperature interaction), $r^2 = 0.780$, $F = 75.5$, df $= 3,64$, $p < 0.001$).

At the Holt roost the same three factors were significant predictors of insect catch. The best fit equation was $\log_e[\text{Insect catch} + 1] = -2.02 + 0.35$ Temperature $+ 1.73$ Light $- 0.107$ (Light intensity × Temperature interaction) [$F = 26.6$, df $= 3,53$, $p < 0.01$]. The similarity in the estimated regression coefficients for the two sites is striking. The four coefficients were not significantly different between the two sites (constant: $t = 0.36$, temperature coefficient: $t = 0.59$, Light coefficient: $t = 0.13$, Interaction coefficient: $t = 0.94$; all $p > 0.05$). Both of these equations describe a surface where the dominant effects on insect catch were light and temperature. At all light intensities the effect of temper-
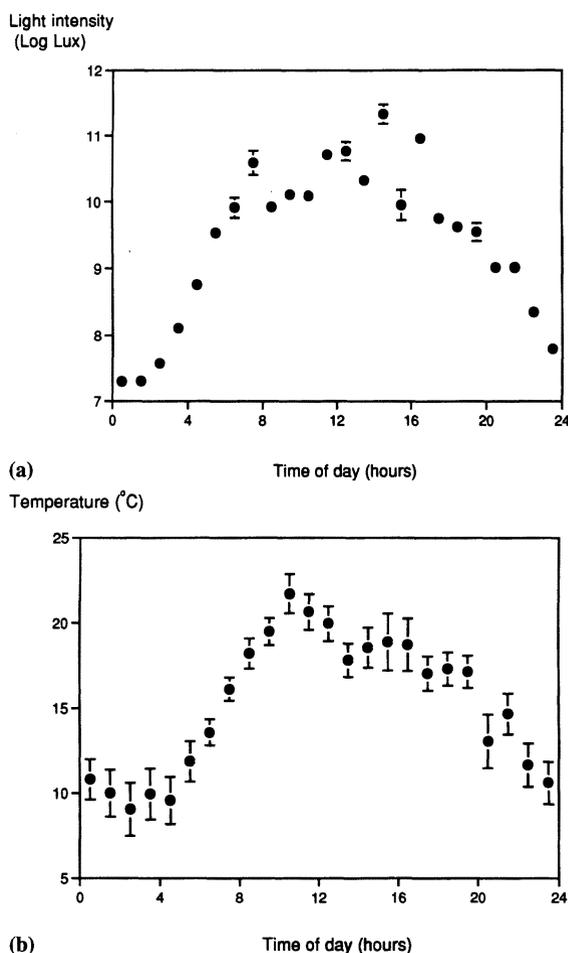

(a)

(b)

Fig. 1. (a) Diurnal cycle in light intensity averaged over 6 d between 10 and 16 July 1991 (Mean ± se). Although it was continuously light the light intensity varied 70-fold between 01:00 when the sun was lowest and the middle of the day. (b) diurnal cycle in temperature averaged over 6 d between 10 and 16 July 1991 (Mean ± se).
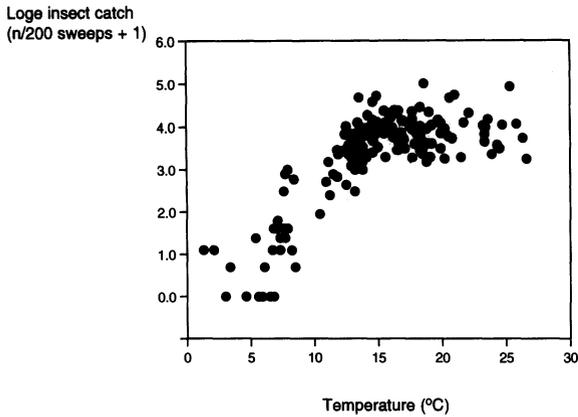
Loge insect catch
(n/200 sweeps + 1)

Fig. 2. Effect of temperature on insect catch at the Kirkesdalen site.

(a)
Percentage Lepidoptera

Time of day (h)

(b)
Mean Wing Length (mm)

Time of day (h)

Fig. 4. (a) Diurnal variation in the activity of lepidopterans as a percentage of total insect catch. There were two peaks in activity (21:00 to 23:00 and 05:00–07:00). (b) mean wing length of insects captured in relation to time of day (Mean ± se). Total measured insects numbered 2300 and in each hour varied from a maximum of 154 at 14:00 to a minimum of 45 at 00:00. The temporal variation was significant.

ature on insect catch was positive, but the magnitude of the effect varied with light intensity, such that at low light intensities temperature had a greater effect than at high light intensities. For example (using the Kirkesdalen equation) a change in temperature from 5 to 20°C, at a light intensity of 1000 lux (typical 'night' values in the present study), would be predicted to increase the insect catch from on average 0.36 to 189.5. However, at high light intensities (40000 lux) the same temperature change would increase the predicted catch from 13.5 to only 49.9.

Throughout the 24-h day, light intensity and temperature varied in a correlated cycle (Fig. 1a, b). There was also a diurnal cycle in total insect catch (Fig. 3). Minimum insect catches occurred between 22:00 and 06:00 and these counts were on average
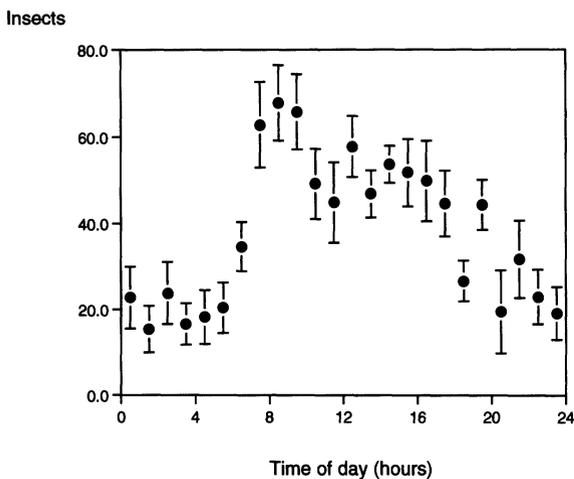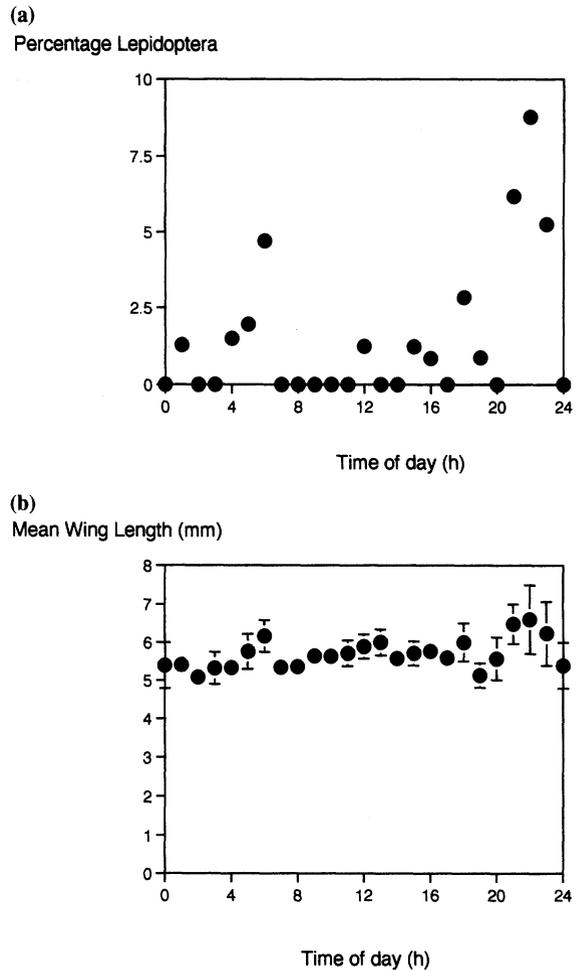
Insects

Time of day (hours)

Fig. 3. Diurnal variation in total insect catch summed across both capture sites (Mean ± se). During the mid-day (09:00–13:00) the catch was 3–4 × greater than the numbers captured between 23:00 and 06:00. The temporal variation was highly significant.

only 20–30% of the catches made between 07:00 and 20:00. This temporal variation was highly significant (ANOVA $F = 3.26$, df $= 23,62$, $p < 0.001$).

The pattern of variation in total insect catch was not mirrored by the variation in numbers of lepidopterans (Fig. 4a). Lepidoptera flew predominantly between 21:00 and 23:00 when they comprised about 9% of the total catch, and between 05:00 and 07:00 when they comprised about 5% of the total catch. At other times of day Lepidoptera were virtually absent. Because of the large sample size the variation in insect size over time was significant (ANOVA: $F = 3.85$, df $= 23,2276$, $p > 0.001$) however the magnitude of the differences was small (Fig. 4b).

sand martins
(Activity at colony)

(a)　　　　　　　　Time of day (hours)
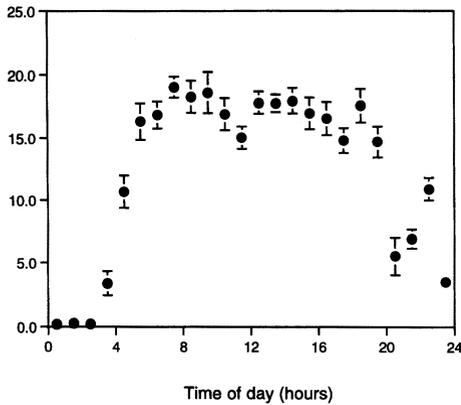
Sand martins
(inactive)

(b)　　　　　　　　Time of day (hours)
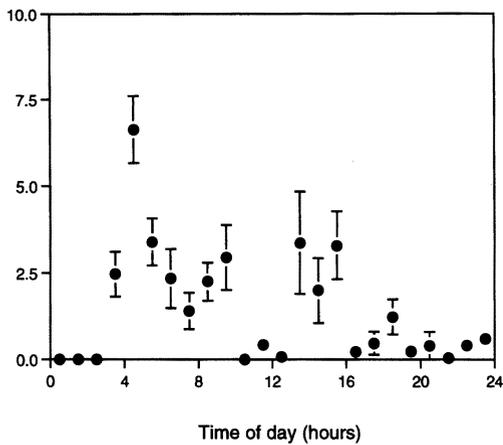
Fig. 5. (a) Average numbers of sand martins entering the colony over 5-min intervals averaged across each hour (Mean ± se). The diurnal variation was highly significant. (b) Average numbers of inactive sand martins sitting on telegraph wires outside the colony (Mean ± se). The temporal variation was significant.

Sand martins

The sand martin colony had 59 holes, of which 29 were definitely occupied by adults feeding nestlings during the study period. The adult nesting population was therefore at least 58 birds, as both male and female parents feed the young. There may also have been other birds incubating eggs, and birds which did not occupy burrows at all. These would include, for example, birds which had attempted to nest but failed. During the study period many adult birds were feeding nestlings which were occasionally observed at the tunnel entrances. There were no flying fledglings evident at the colony.

Birds in the colony exhibited a diurnal pattern of entrance activity (Fig. 5a) and were least active between 23:00 and 03:00. Thereafter, activity increased to around 20 entrances per 5 min, at 07:00, which was maintained throughout the day, until around 20:00. Between 20:00 and 23:00 activity was reduced. Between 07:00 and 20:00 the coefficient of variation in the counts, in each hour, varied between 29 and 46%, and averaged 37.6%. Since the error rate in counts was about 8%, this indicated that most of the observed variance in the hourly entrance counts was due to biological factors, rather than counting error.

The numbers of birds sitting on the telephone wires not foraging, varied between 0 and 23. Assuming a minimum population of 58 birds, up to 40% of the colony might be out, but not flying, at any one time. There was significant temporal variability in the numbers of birds on the wires (Fig. 5b: ANOVA $F = 1.88$, df = 23,40, $p = 0.039$). The peak numbers were recorded between 03:00 and 07:00, thereafter there were fewer birds on the wires.

The pattern of activity per hour, averaged across days, was non-linearly related to the pattern of insect availability summed across the two roosts (Kirkesdalen 6 km away and Holt 20 km away from the sand martin colony), also averaged across days. The effect was non-linear and the best-fit regression explained 68.6% of the variation in sand martin activity (Fig. 6). Hourly mean sand martin activity (not averaged across days) was entered as the dependent variable in a stepwise multiple regression (forward inclusion, with retrospective deletion, p to enter or remove = 0.05) with log insect availability (catch + 1), light intensity, temperature, number of birds on the wires, and all the two-way interaction terms as independent predictor variables (none of the predictor variables were correlated with an r^2 of greater than 40%). The best fit equation, explain-
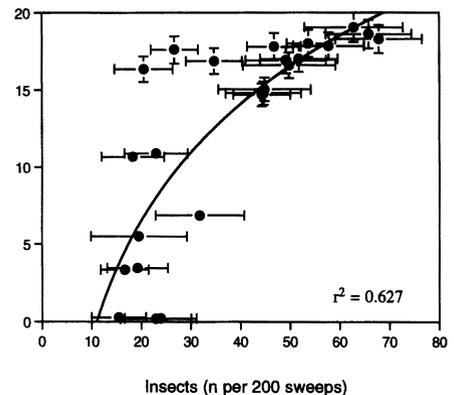
sand martins
(nest activity)

Insects (n per 200 sweeps)

Fig. 6. Relationship between sand martin activity for each hour averaged across days (Mean number entering per 5 min ± se) and insect catch averaged across the same hour (Mean catch across both sites ± se). There was a significant non-linear relationship shown by the fitted curve ($r^2 = 68.6\%$).

80

a)

bat activity

Kirkesdalen roost

b)
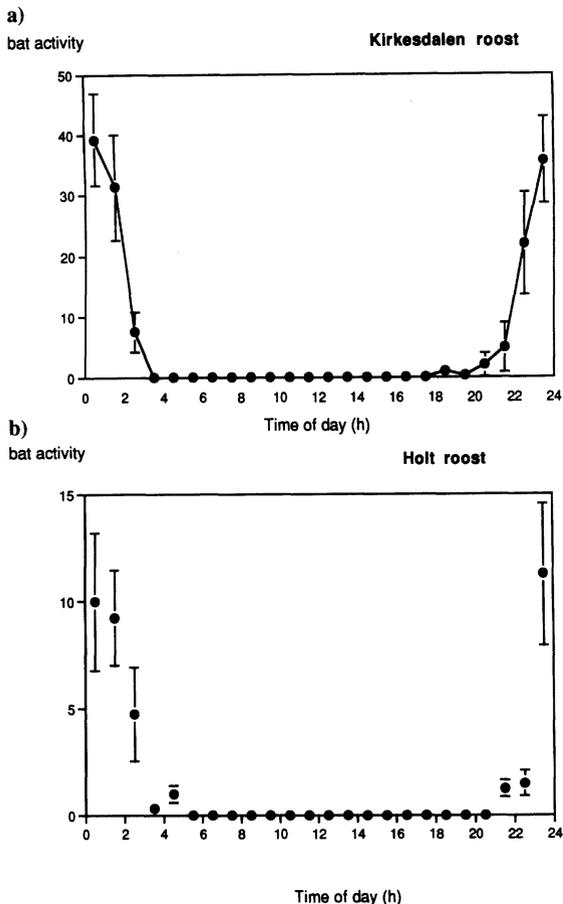
bat activity

Holt roost

Fig. 7. Activity of bats (summed entrance and exit events in each hour averaged across days) (a) Kirkesdalen roost and (b) Holt roost.

ing 64.0% of the variability in sand martin entrance activity was: Entrances per 5 min $= -44.0 + 16.3$ $\log_e$(Temperature) $+ 26.0$ Light $- 7.12$ (Light × temperature interaction) ($F = 34.4$, df $= 3,58$, $p < 0.001$). The residual variation (36.0%) was much greater than the error in these measurements (8%) suggesting that other biological factors, which we did not account for, were also influencing the entrance activity of these birds. Four measurements of activity when goshawks were present at the colony and activity fell to 0 are excluded from this analysis.

Northern bats

We analysed the emergence data from the two roosts separately.

Kirkesdalen

All entrance and exit activity at the roost occurred between 18:00 and 03:00 (Fig. 7a). Most activity occurred between 22:00 and 02:00. Bats were continually

active at the colony throughout the activity period, suggesting they did not travel far from the roost when foraging. Bats coincided their periods of feeding behaviour with the time when insect availability was at its lowest (Fig. 3). Bat activity also coincided with the period when sand martins were least active (Fig. 6) and the time of day when it was coolest (Fig. 1b) and light intensity was lowest (Fig. 1a).

Bat activity (summed entrances and exits in each hour) was entered as the dependent variable in a stepwise multiple regression (forward inclusion with retrospective deletion, p to enter or remove $= 0.05$). The best fit equation was: Bat activity (Kirkesdalen summed entrances and exits per hour) $= 78.41 - 69.65$ Light intensity $+ 13.41$ (Light intensity)$^2 + 2.66$ Insect catch [$r^2 = 0.59$, $F = 30.9$, df $= 3,64$, $p < 0.001$]. This equation describes a surface where light has a dominant role influencing the activity patterns of the bats. At high light intensities the predicted activity of the bats was zero, and independent of the abundance of insects. The sharply non-linear effect of light intensity suggests a critical threshold intensity below which bats are active outside the colony, and above which they are not. Below this threshold, there was a positive effect of insect catch on activity. Although the cycle of bat activity was coincident with the lowest period of sand martin activity (6 km away), and also the coolest temperatures, these two factors were not significant predictors of the timing of bat activity at the colony.

To further illustrate the effects of light intensity on the activity of the bats we present three time courses of emergences from the colony recorded on 14, 10 and 13 July, respectively (Fig. 8). On 14 July the net number of bats absent from the colony increased at around 22:00 when the light intensity was 2400–3000 lux. On the 10 July it remained brighter much longer, and the light intensity did not fall below the threshold value of 2400–3000 lux until about 23:40. The bats did not emerge until 23:30, a full 90 min later than on 14 July. On the 13 July the light intensity oscillated, first it started to decline and fell below 2400 lux at about 21:40. Between 21:40 and 22:30 11 bats left the colony. However, the occurrence of an unusual cloud formation which reflected large amounts of light from the sun meant light intensities increased above 3000 lux, at about 22:40, and remained elevated until about 23:50. Eleven bats, presumably those which had left between 21:40 and 22:30, returned into the colony between 22:30 and 22:50, and no further net emergences were recorded until 00:00–00:20, when 41 bats emerged. This emergence of 41 individuals was the largest net number of bats absent from the roost during the study period, and represents the minimum colony size.

We divided the potential exit directions from the roost into six zones which varied in their distance to the nearest trees, from 3 m to 200 m. There were significant inverse relationships between the distance to trees and

the number of bats leaving or returning in that direction (Fig. 9). Fresh bat droppings collected at the Kirkesdalen roost were dominated by dipterans. The faeces comprised 88% Diptera by volume, 8% Lepidoptera and 4% unknown.

Holt

Fewer bats were in the Holt colony, and hence activity (summed entrances and exits) was also lower. The minimum colony size was 14 bats. The diel pattern of activity at the Holt roost (Fig. 7b) was similar to that at the Kirkesdalen roost (Fig. 7a). Hourly activity at Holt was significantly correlated with the simultaneous activity recorded at Kirkesdalen, $r^2 = 66\%$, $n = 58$. If the daytime paired zero values, which make the distribu-

Bats in or out
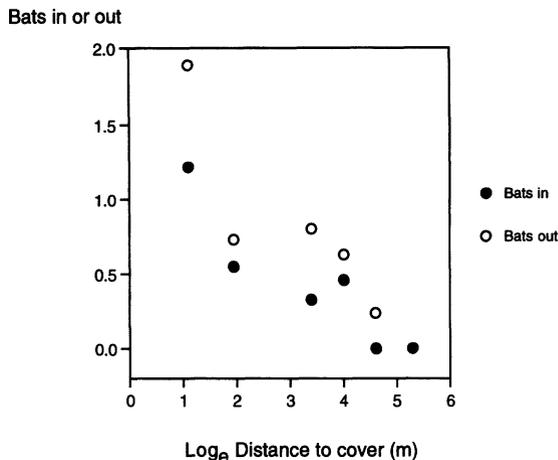
Fig. 9. Relationship between distance to tree cover and the numbers of bats leaving or entering the Kirkesdalen roost to or from that direction. Totals are summed across all activity periods. Entering numbers are lower than exiting numbers because it was not always possible to assign a direction to a returning bat. The relationships for both ins and outs were significant.

tions non-normal, are excluded then the r^2 falls to 44%. We entered the hourly summed entrance and exit activity at Holt as a dependent variable in a stepwise multiple regression (forward inclusion with retrospective deletion, p to enter or remove = 0.05). The best fit equation was: Bat activity (summed entrances and exits per hour) = $6.726 - 5.43$ Light $+ 1.32 \log_e$ Insect catch ($r^2 = 41.7\%$, $F = 18.24$). The equation derived for the Holt roost explained less of the variability in the bat activity, and also had a different form than the equation derived at Kirkesdalen. These differences probably reflect, first, the lower activity at the Holt roost, the smaller sample of hours of observation and the fewer number of bat activity periods included (four as opposed to six). Nevertheless the same strong negative effect of light intensity combined with a positive effect of insect catch was found.

Raptors

In total we observed raptorial birds 62 times during 237.5 h of observation. The majority ($n = 46$) of the observations were of rough-legged buzzards (*Buteo lagopus*). Other species recorded were hawk owls (*Surnia ulula*; $n = 7$), northern goshawks (*Accipiter gentilis*; $n = 4$), European sparrowhawks (*Accipiter nisus*; $n = 3$), and European kestrels (*Falco tinnunculus*; $n = 2$). There were insufficient data to analyse the temporal variation in activity within species. There were differences in the numbers of hours of observation made in each two-hour period throughout the day; therefore, we normalised the data for observation intensity. We recorded the number of birds seen in each two hours, and then

a) 14/7

Light (lux/500) and Emerged bats

b) 10/7

Light (Lux/500) and Emerged bats

c) 13/7

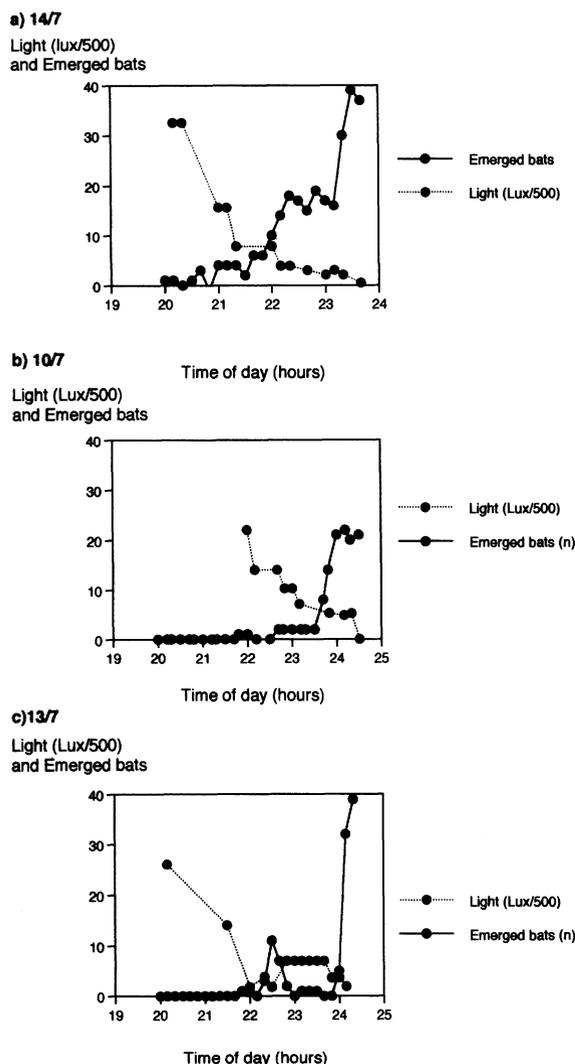Light (Lux/500) and Emerged bats

Fig. 8. Effects of changing light intensity on the emergence behaviour of bats at the Kirkesdalen roost. (a) 14 July 1991 (b) 10 July 1991 and (c) 13 July 1991. In each case light intensity and the net number of bats emerged from the colony are shown as a function of time.

recalculated the expected numbers that would have been observed if we had made observations for equal time periods in each interval, by multiplying the observed rate in that interval by the mean time across all bi-hourly intervals (19.6 h) (Fig. 10). Temporal variation over the 24-h cycle in summed raptor activity was not significant ($G = 12.87$, df $= 11$, $p > 0.05$).

Discussion

Aerial insect activity

Variation in the replicate insect catches within each hour was high (39%). The major factor contributing to the low repeatability was probably the patchiness in insect spatial distributions. Sweep netting does not provide an absolute measure of aerial insect abundance, and caution should be applied when interpreting the availability of aerial insects when sampled in this manner, particularly when there is only one observer and the variation in replicate catches is not assessed. Nevertheless, in the current study the range of temporal variation in mean insect catches (three- to four-fold, Fig. 3) was an order of magnitude greater than the replication variation. We are confident therefore that diurnal variation in insect catches was not a sampling artefact.

Previous studies in the north temperate regions have also shown that flying insects are predominantly active during the day (Williams 1961, Lewis and Taylor 1965, Rydell 1992, Speakman 1995, Rydell et al. 1996). Hence, the pattern in northern Norway was unlikely to be unique to the area, or to the period of constant

daylight. The effect of temperature on flight activity was also consistent with previous studies (Taylor 1963, Lewis and Taylor 1965). There is a threshold air temperature below which insects are unable to fly, which varies with taxa between 5 and 13°C (Alma 1970, Cockbain 1961, Taylor 1963). Consistent with these thresholds, at our sites insect catches declined when air temperature fell below 14°C (Fig. 2a). The effect of temperature interacted with light intensity, so that at low light levels the effect of temperature was far more pronounced. The reasons for this interaction remain unclear.

Sand martins

It was not possible, from the entrance rate data, to directly assess the numbers of birds which were out of the burrows and flying around, since variation in the entrance rate could reflect changes in several different parameters. For example, increases in the time spent foraging, time spent out of the burrows but not foraging, and the time spent inside the burrows, would all tend to decrease the rate at which the martins entered the holes. During the period between 24:00 and 03:00 we suspect that birds were all in burrows, since the first activity of the morning consisted of birds exiting the burrows with no evidence of immediately preceding entrances, and during this period we saw no birds flying around outside the colony, or sitting on wires (Fig. 5b). The low activity at the burrow entrances between 03:00 and 06:00 (Fig. 5a) was at least partly due to some of the birds being out of the burrows but not feeding their young, since this was the time when the peak numbers of birds were recorded on the wires (Fig. 5b).

There was an apparent temporal concordance between the activity of sand martins (averaged across days) and the pattern of daily variation in insect availability which followed the classical form of a functional response (Holling 1959) (Fig. 6). However, insect availability was not a significant predictor of the hourly records of sand martin activity, perhaps because insect availabilities were measured at the two bat roosts 6 and 20 km away, and not where the martins were feeding. Light and temperature measured immediately adjacent to the sand martin colony were the major factors influencing sand martin activity. These same two factors were the major parameters influencing insect availability at the two bat roosts. The primary factor influencing the activity of the sand martins at their burrows may have been local insect abundance, but our direct measures of insect catch in any hour at the bat roosts may have been less accurate reflections of the abundance of insects at the sand martin colony, than the immediately local variation in temperature and light levels. An alternative explanation is that direct measures of insect catches in sweep nets were only poorly

Raptors
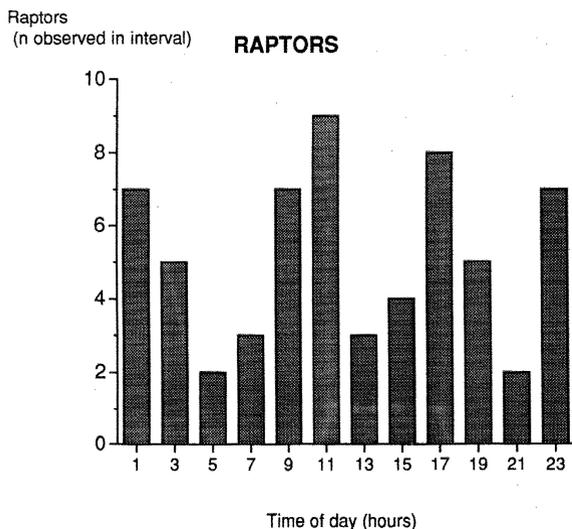(n observed in interval)

RAPTORS

Fig. 10. Temporal variation in observations of flying raptors (hawks, falcons and owls) throughout the study area corrected for variations in the number of observation hours in each bi-hourly period. The temporal variation was not significant.

related to availability of insects to the birds, which might also be affected directly by light intensity as they orient visually. Low light intensity influences foraging efficiency of other small insectivorous birds, for example great tits (*Parus major*) (Kacelnik 1979), but experimental demonstrations of effects in nighthawks were equivocal (Brigham and Barclay 1995). Activity of sand martins at the colony was consistent with the birds timing their foraging behaviour to coincide with maximum abundance of their prey.

Bats

In Sweden, at 57 and 65° N, where there is true night all summer, the activity of *Eptesicus nilssonii* coincides with darkness (Rydell 1989, 1992). If risk of predation was the major factor influencing chiropteran nocturnality (Speakman 1990, 1991a, b, 1995, Speakman et al. 1994a, Rydell and Speakman 1995) the absence of temporal variation in raptor activity (Fig. 10), in combination with the diurnal cycle of insect availability leads to the prediction that the bats at our study site should adjust their peak activity from 22:00–02:00 to 08:00–12:00. That is, once the benefits of darkness were removed because the risk of predation was equalised over the 24-h period, the bats should have foraged when prey were most abundant. In contrast, if competition with insectivorous birds was the dominant factor (e.g. Tugendhat 1966, Ollason et al. 1992), we predicted that the bats would be most active between 23:00 and 05:00 when the sand martins were least active (Fig. 5a). The bats conformed most closely to this latter prediction, being most active between 22:00 and 02:00.

Rydell (1989) has shown that in southern Sweden, in July, northern bats eat considerable numbers of Lepidoptera. Perhaps the bats timed their activity not to coincide with peak total insect availability, which was dominated by small dipterans, but the peak activity of Lepidoptera, which was greatest between 21:00–23:00 and between 04:00 and 07:00 (Fig. 4a). These peaks preceded and followed the peak in bat activity and did not coincide with it. In addition, our fecal analysis suggested the bats were feeding on small dipterans and not lepidopterans.

The timing of bat foraging activity was more consistent with the competition hypothesis, than the predation hypothesis. Although the bats were not active for the entire time that the sand martins were inactive this may have been because they were able to meet their energy and nutrient requirements during the period they were active, and had no need to forage for the entire night. Further evidence supporting the competition hypothesis is the faecal analyses which suggested the bats fed predominantly on small Diptera, which are the dominant prey of sand martins in northern latitudes (Turner 1982).

However, the competition hypothesis is less consistent with the fact that densities of both the bats and insectivorous birds were very low. We never observed a sand martin in the vicinity of either bat roost, and never observed a bat in the vicinity of the sand martin colony. It is difficult to imagine therefore where competitive interactions restricting bat activity to the 'night' might take place. It is possible that the birds and the bats shared a single common feeding ground, but that seemed unlikely. Most of the sand martins were observed feeding at the Malselv river immediately adjacent to the colony (< 1 km away), where we never observed bats, and the continuous activity of bats at Kirkesdalen (6 km from the sand martin colony) suggested they were feeding close to the roost. We observed bats feeding at sites 500 and 1000 m from the roost at Kirkesdalen, but never greater than 2 km away, although our searches were not comprehensive. We occasionally observed other aerial insectivorous birds in the vicinity of the bat roosts, but from a total of 159 h of observations they were present for less than 10 min, and were thus unlikely to be a competitive constraint on the bats. Perhaps in the recent past densities of both bats and insectivorous birds were higher, and the activity patterns we observed were a legacy of this earlier competition. Although we are aware of no historical population data for our study area, sand martin populations throughout the rest of Europe declined enormously during the 1980s because the Sahel drought reduced their survival during migration (Jones 1987). Assuming population changes at our study site were similar this would be consistent with the 'ghost of competition past' idea.

Although bat activity was most consistent with the competition hypothesis the close correlation of bat activity with light intensity raises three other possible explanations for their activity patterns. First, the light intensity may have reflected the heat burden that is placed on the bats by solar radiation. This seems improbable because we would expect ambient temperature to also be a factor influencing the pattern of activity if heat burdens were important, but it was not. In addition the temperatures and solar elevations were both relatively low. At low sun elevations (30–40°) the predicted critical ambient air temperatures, above which bats would be unable to fly because of the risk of hyperthermia (Speakman et al. 1994b), are 35–37°C, yet ambient temperatures were about 20–30°C lower than this (Fig. 1b).

Second, variations in light intensity may have influenced the risk of predation. All the raptorial birds recorded in this study were visual predators. The discriminant abilities of raptors are strongly dependant on luminance (Fox et al. 1976). Hence their ability to capture a bat may possibly have been related to the light intensity. Although raptorial birds were continuously active throughout the diurnal cycle (Fig. 10), this

does not necessarily mean the risk of predation to a flying bat was constant. The frequency that different directions were used by bats as they left and returned to the Kirkesdalen roost (Fig. 9) could be interpreted as indicating these bats were susceptible to predation, even when they emerged in synchrony with the darkest period of the day. Nyholm (1965) observed that Daubentons bats (*Myotis daubentonii*), in the far north of Finland (60° N), avoided open water habitat when feeding around the summer solstice, when the night was shortest, and the sky lighter, but fed in this habitat later in the year when it was darker. Similar data were reported by Rydell (1992) in northern Sweden (65° N). These data are also consistent with an anti-predator response, but could also reflect changes in insect distributions at different times of year.

Although discriminant abilities of falcons are strongly dependent on luminance (Fox et al. 1976), the extent to which predation risk declined with light intensity is uncertain. Minimum light levels reported here were considerably higher than the light levels at which bats emerge further south (Jones and Rydell 1995, Speakman et al. 1995) and it is well established that diurnal predatory birds can successfully attack such emerging bats (Gillette and Kimborough 1970, Fenton et al. 1994). Directly testing whether the predation risk varies with time of day would be extremely difficult. This is because predatory events are only very occasionally witnessed, and no natural predation on bats could be witnessed during the day because the bats do not naturally emerge at this time. If bats are forced to emerge in daylight they immediately re-enter the roost. We confirmed this effect, after the activity studies were completed (16 July), by entering the Kirkesdalen roost and over a period of 50 min we forced a total of 39 bats (possibly including some repeat exits) to leave in the middle of the day. All but two of these bats immediately (within seconds to one minute) re-entered the roost.

Finally, our analyses of the activity patterns of these bats have focused on functional interpretations of their behaviour. Perhaps, however, these bats routinely synchronise their activity with darkness during the remainder of the summer, when there is a true night, because of similar pressures which affect other nocturnal bats (Speakman 1995). During the period around the solstice they may be unable to break out from entrainment to this stimulus. Consequently, there may be no immediate benefits attached to coinciding their activity to the darkest period of the day around the solstice. This latter interpretation would also be difficult to test. However, other bat species faced with changed selective pressures have managed to overcome entrainment to darkness (e.g. the Azorean bat *Nyctalus azoreum*; Moore 1975 and the Samoan fruit bat *Pteropus samoensis*; Thomson et al. 1998).

In summary, the activity patterns of the bats in northern Norway are less clearly understandable than the activity patterns of the sand martins. The overall pattern was closest to that predicted by the competition hypothesis. The low densities of both the bats and aerial insectivorous birds were inconsistent with this hypothesis but the pattern could reflect competition between historically higher populations. The bats appeared to synchronise their activity with the darkest period of the day. This was unlikely to have been a consequence of risks of hyperthermia, but might possibly reflect an anti-predation strategy. An alternative interpretation is that bats were entrained to forage in the darkest part of the day by their behaviour during the period of the year when there is a true night, and there were no immediate benefits associated with the behaviour around the period of the solstice.

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