Influence of night length on home range size in the northern bat *Eptesicus nilssonii*

Karl Frafjord

Tromsø University Museum, University of Tromsø, NO-9037 Tromsø, Norway

e-mail: karl.frafjord@uit.no

tel. +47 776 45725

Running heading: Night length influences home range

ABSTRACT

The northern bat *Eptesicus nilssonii* is widespread in Fennoscandia, with breeding populations well above the Arctic Circle. I studied this species at its extreme northern limit, at 69 °N in Norway. I radio-tracked 17 bats from 2 maternity roosts during 2003-2006 to study the influence of the midnight sun and increasing lengths of darkness on activity (time spent out of roost) and home range size. Activity and home range was highly correlated with night length (light intensity); both increasing progressively with season. Bats were classified into 3 groups based on the time of the season they were tracked (basically July, August and September-October); short activity (average 1.57 hours) and small home range (average 0.91 km^2), medium activity (3.69 hours) and medium-sized home range (4.58 km^2), and long activity (4.80 hours) and large home range (17.2 km^2). Bats visited roosts several times during the night, and the duration of roost visits increased significantly by group. The number of periods out of roost increased from the first to the second group (1.45 vs. 2.36 flight periods per night), but insignificantly to the third group (2.37 flights). The most significant increase in activity and home range was associated with the first flight of juveniles in early August. These bats appeared to have a threshold level of around 1700 lux for activity out of roost, with little difference between light levels at emergence and return (the second group returned in significantly poorer light than they emerged in). Although the northern bat at this extreme latitude had adapted to the ambient light conditions, the bright nights under the midnight sun and the short season strongly reduced their window of opportunity for activity and may possibly reduce survival and reproductive success.

Key words: Chiroptera, Activity, Extreme north, Home range, Night length

Introduction

Predation is a prominent feature that shapes the foraging ecology of small mammals and risk reduction is important for prey animals. Animals must weigh the benefits of energy and nutrient intake against the cost of increased vulnerability to predators during foraging (Halle and Stenseth 2000). Bats (Chiroptera) have evolved many special adaptations, one of which is nocturnal foraging (Rydell and Speakman 1995; Altringham 2011; Boyles et al. 2007). Why bats prefer to hunt at night has been a subject of discussion, but it is obviously an integral part of their evolution. Three main hypotheses have been proposed to explain the nocturnal behaviour of bats. According to the predation hypothesis, a synchronized emergence may confuse predators and reduce the risk to individual bats, as many bats appear to be most vulnerable at dusk. Foraging at night can be an effective strategy to avoid diurnal birds of prey, although it would increase exposure to owls. By hunting at night, bats also reduce competition with insect-eating birds (the competition hypothesis). The third hypothesis is the risk of hyperthermia, overheating, if bats fly during the day (Speakman et al. 1994; Russo et al. 2011a). Most reports point to the avoidance of raptors as the main reason why bats choose to be active at night (Fenton et al. 1994; Jones and Rydell 1994; Rydell and Speakman1995, Rydell et al. 1996; Duvergé et al. 2000; Speakman 2001, Russo et al. 2007).

Foraging flights may account for half the energy budget of a reproducing bat (Barclay 1989; Rydell 1993; Speakman and Thomas 2003), so bats need to forage efficiently. Furthermore, they hunt during the night when the abundance of aerial insects is generally smaller than during the day (Rydell 1986, 1992; Speakman et al. 1992, 2000; Rydell et al. 1996, Russo et al. 2011b). Most studies of home range size in bats have discussed their results in relation to reproduction. In a study of the little brown bat *Myotis lucifugus*, home range size was reduced by 51% between pregnancy and lactation, possibly from the need to return to roosts at night to nurse (Henry et al. 2002). Mammals of this size may produce up to 25% of their body mass in milk daily and may need to download this to their offspring frequently, but how these bats distribute their nursing bouts during the 24-h cycle is unknown. Henry et al. (2002) concluded that increased insect availability allowed lactating bats to forage closer to the roost without increasing their foraging time, despite greater food requirements during lactation. Similarly, O'Donnell (2001) found that lactating long-tailed bats *Chalinolobus tuberculatus* used significantly smaller ranges than both post-lactating and non-reproducing females. In the big brown bat *Eptesicus fuscus*, Wilkinson and Barclay (1997) found no significant difference in foraging time between pregnant and lactating females or between females and males, but males used larger and potentially less productive ranges than females. De Jong (1994) studied the northern bat *E. nilssonii* in central Sweden and found a large increase in home range size and foraging time during the summer. Rydell (1993) found that foraging time of northern bats in southern Sweden increased by 100% from pregnancy to lactation, while non-breeding females showed no such increase (sensu Racey and Speakman 1987). The northern bat has been found to emerge later relative to sunset during the last part of pregnancy and first part of lactation (Duvergé et al. 2000).

Few bats live north of the Arctic Circle (66°33' N; sensu Parker et al. 1997), where the summer is dominated by midnight sun and perpetual light. The most widespread bat in Fennoscandia is the northern bat, which extends its breeding range in Norway to 69 °N latitude (Rydell 1992; Rydell et al. 1994; Frafjord 2001). Only two other species have been recorded at the Arctic Circle, Daubenton's bat *Myotis daubentonii* and Brandt's bat *M. brandtii* (Siivonen and Wermundsen 2008). At high latitudes, the bright mid-summer nights may limit the time available for foraging and consequently influence both survival and reproduction. A shorter foraging season may limit opportunities to build fat layers to survive long hibernation periods, putting special demand on reproducing females.

I studied the northern bat at the northern edge of its distribution. My goals were to study their home range and the influence of night length on home range size and activity. Although the bats may have been energetically constrained by reproduction as outlined above, I sought to study the influence of bright nights as an extreme condition for a nocturnal bat, the influence of an increasing night length and, to a lesser extent, the influence of reproduction. The study was spread over the entire season when bats were known to be active. I also sought to locate hibernation sites (Frafjord 2007), hence the study continued well into the autumn. I predicted that 1) home range and activity would increase initially, but then reach an asymptotic level or perhaps decrease, 2) length of night would have a profound impact on timing and length of activity, but less on home range size, 3) the longest activity (foraging) period would occur in early August, before the initial flights of the young (prior to weaning), 4) the nightly visits to roosts would be most frequent before weaning, and 5) lower temperatures as season progressed would reduce activity and home range.

Materials and methods

Study area

This study was conducted in southern Troms, northern Norway (approximately 69° 00’ N, 19° 00’ E), a region with relatively warm summers and cold winters (down to -40 °C). On overcast nights, temperatures in summer (June-August) were generally 5-15 °C. Due to temperature inversions, however, the temperature frequently reached zero at ground level on clear nights. At this latitude, there are two months of midnight sun (about 23 May to 19 July), when the sun does not set below the horizon. Throughout this paper the terms “night” and “nocturnal” refers to the bats’ general activity period, a proxy for bats being out of the roost. Hence, I also use “night” for the first period when the sun does not set below the horizon (the “polar day”), but generally “set” behind hills. Otherwise, “night” refers to the period between sunset and sunrise, also including civil twilight when the sun is ≤ 6 ° below the horizon.

The main habitat in this region is boreal forest (pine *Pinus silvestris* and birch *Betula pubescens*) interspersed with farmland, the tree line is generally around 500 m a.s.l. and the highest peak is about 1500 m a.s.l. (see also Rydell et al. 1994). The region is sparsely populated.

I studied bats from two different maternity roosts in two neighbouring valleys, both in occupied houses. Roost 1 contained about 100 adults during the study period, where the bats mainly occupied the roof above the unheated attic (the roof was heated by the sun in a clear sky), whereas Roost 2 had 10-15 adult bats, where the bats mainly lived in the walls close to heat sources. The valley where Roost 2 was situated is narrow, about 1.5 km across, the other is much wider. Bats in this region are generally active and found at roosts between the spring and autumn equinoxes (sensu Rydell 1989), but very few can be found before 1 July and some are active until mid-October. Most young generally start to fly in the first half of August, and are hence born in the middle of July, but variation may be large and the latest are born in early August.

Animals and radiotracking

A total of 17 northern bats were trapped in a harp trap at the two roosts during the years 2003-2006 (Table 1) and radio tags (Biotrack Ltd, PIP3, 0.45 g) were glued to their backs (Medical Grade Adhesive PSA 40086, Sikema AB) after trimming the fur. Typically, only one bat was radio-tagged at any given time, but in two cases I followed two bats simultaneously for a short period, whereby I tracked each on every second day. Because my intention was to cover the complete season that bats are active in this region, bats were tracked from early July until the middle of October. I intended to follow every bat ≥10 days, and focused on sampling good data for individual bats rather than tracking a large number of bats. Some tags fell off prematurely which resulted in fewer nights than optimal; these cases are included in some analyses or illustrations for which the data was adequate (Table 1). From 2005, increased longevity of the transmitter (reduced signal length and increased interval between signals) increased battery longevity to one month enabling longer tracking periods. From 2004, I mainly used the receiver FM-100 (Advanced Telemetry Systems, Inc., USA), with either a 2- or 3-element Yagi antennae (Televilt International AB, Sweden) and always with headphones. The radio signals were monitored continuously during tracking unless I actually saw the bat. Hibernating bats were not tracked every night.

I followed every bat as close as possible, homing in as close as roads and terrain permitted. This meant that I frequently observed the bat, and was typically within 500 m of it. The bats' movements were monitored continuously, with new positions (and distance) verified by triangulation as often as needed. As the bat was constantly on the move reasonably close by, triangulation was frequently possible from a single location, the position of which was recorded by a handheld GPS unit (Garmin GPSMAP 60Cx). Special attention was given along the edge of a bat's hitherto known range. Most bats were followed during their entire periods of flying for as long as the transmitter worked or stayed on the bat. I followed bats on foot, on bicycle or by car as circumstances required. I rarely lost track of a bat for any length of time.

Data analysis

This labour-intensive tracking method implied that few bats could be tagged. Statistical tests used were 1-way ANOVA with Tukey post hoc tests (note that results from post hoc tests are not reported in full and should be judged with caution, because of the risk of Type I error with small samples), Wilcoxon's z, Spearman's correlation and regression in the software IBM SPSS Statistics. The ANOVA test was used to test for differences between three groups of bats (see below). Means are given ± 1 SD. Because of the intercorrelation between many of the variables analysed, I did not use any multiple-variable test. The units of analyses were either individual bats or individual nights. When needed, I used the median date of each tracking period. The bats were grouped in three temporal groups by this median, basically July (Group 1), August (Group 2), and September-October (Group 3). This was done as a substitute for reproductive status or demographic groups, and enabled comparisons of bats in different light conditions. I included the following eight intrinsic variables (Table 2):

1) Home range size: 100% minimum convex polygon (MCP), estimated by the software Tracker ver. 1.1 (sensu Lawson and Rodgers 1997). MCP was used to enable the estimation of the actual size and shape of the area used by each bat, including even a few “irregular” movements (“outliers”) in the autumn.

2) Maximum diameter: the largest distance from one end of the home range to the opposite end.

3) Mean time out: the time a bat was out of roost (between exit and return = the total active period) was estimated for every night and averaged first for each bat and then for all bats. A few brief pauses out of roost are included, but not time in hibernation (see results). Only active periods lasting more than 5 minutes were included in all analyses. Shorter periods were excluded, i.e., when the bat attempted to leave the roost, but quickly returned due to bad conditions (heavy rain or low temperatures).

4) Maximum time out: the longest time out of roost among all the nights a bat was tracked. In autumn, this maximum may be more interesting than the mean, which is influenced by nights with inclement weather.

5) Mean number of active periods: the number of periods a bat was active, i.e. active periods outside roosts interrupted by visits to the roost.

6) Maximum number of active periods: the maximum number of periods out of roost among all the nights a bat was tracked.

7) Duration of roost visits: duration in minutes of roost visits, the sum of the time spent inside the roost during the active period calculated as the sum of all visits each night.

8) Body mass: mass at capture. Bats were weighed using a spring scale (0.5 g graduation) while held in a cotton bag.

I also included the following five extrinsic variables (Table 2):

1) Temperature at exit: air temperature when the tagged bat first emerged from the roost, measured to the nearest 0.5 °C using a thermometer placed approximately 1 m above ground. In 2003, I largely used temperature and light intensity measured by a datalogger placed close to Roost 1 that operated automatically throughout the season (Pace Scientific, Inc., XR440 with light sensor and temperature/relative humidity probe, logging a reading every 5 minutes).

2) Temperature at return: temperature when the tagged bat last returned to the roost (i.e. entered the house), measured as above.

3) Lux at exit: light intensity when the tagged bat first emerged from the roost, measured using a handheld meter (Extech Instruments Pocket Foot Candle Light Meter, Model 401027). The sensor was held high up and pointing towards the brightest part of the sky so that maximum light intensity was recorded. The original measurements in foot candles were used in statistical analyses and then converted to the SI unit lux (foot to meter conversion).

4) Lux at return: light intensity when the tagged bat last returned to the roost, measured as above.

5) Length of the night: the length of the period between sunset (sun below the horizon) and sunrise (sun above the horizon), as defined by the latitude for the study site. Night-length is zero for the first period with the sun above horizon all 24 hours.

Results

Of the 17 bats tagged, 16 were females and 1 male, 12 adults and 5 juveniles (Table 1). Good quality data were collected from 13 bats, limited data from 2, and scarce data from 2. I found a large variation in home range size, from less than 1 km^2 to more than 20 km^2 (Table 1). The ranges increased progressively through summer and autumn, with the smallest ranges during the first part of the season. The smaller ranges were not circular around the roost, but were distributed in oblong sectors with small to large overlaps between individual bats (Figs. 1a-c). The larger ranges were elongated along the two valleys, as none of the bats ventured high up the slopes. The increase in home range size was exponential, with the rapid change starting in early August. This pattern was almost identical to the relationship between home range size and night length (Fig. 2). A significant correlation in home range size with time of the season (day-month converted to a metrical scale) was found ($r=0.95$, $n=13$, $p<0.01$). This is best illustrated when the bats were divided in three temporal groups. Average home range size was about 1 km^2 for Group 1, 4.5 km^2 for Group 2, and 17 km^2 for Group 3 (Table 2). Home range size was also closely related to the length of the nightly active period (Fig. 2). It was also positively correlated to most of the intrinsic variables (variables 2-4: $r=0.98$-0.91, $p<0.001$, variables 6/7: $r=0.70/0.75$, $p<0.01$, variable 5 (average number of periods out): $r=0.57$, $p<0.05$; $n=13$ in all cases), the only exception being body mass ($r=-0.39$, $p>0.05$), and negatively correlated to the four extrinsic variables other than night length ($r=-0.85$--0.79, $p\leq0.001$).

All variables behaved similarly to home range size, with significant differences between the three groups except in body mass (Table 2), and all were significantly correlated with time (most variables: $r=0.79$-0.98, $p<0.01$, for average number of periods out: $r=0.58$, $p<0.05$, and for maximum number of periods out: $r=0.53$, $p<0.05$). Tukey post hoc tests revealed that Group 1 differed ($p<0.05$) from both Group 2 and 3 in all intrinsic variables except home range size and maximum number of periods out. For these two variables, Group 1 was significantly different only from Group 3 (due to the risk of Type I error with small samples all results from these tests are not reported). Thus, length of the active period, number of active periods and duration of roost visits all increased with season, while the temperature and light intensity decreased. Consequently, night length is probably the major common factor associated with these seasonal changes (Fig. 3). In July, under the midnight sun, bats were active for 1.5 hours on average and the maximum time out was a little more than two hours (Fig. 4). In August, as the night started to darken, the bats limited their active period to between sunset and sunrise, while later the length of the dark night exceeded the needs of bats (Table 2), even for their maximum time out (Fig. 4). Maximum time out for Group 3 was almost nine hours (Table 2), and the record was one bat flying continuously for 10.3 hours without a single roost visit or pause. When bats were out of the roosts (active) they appeared to be searching and hunting continuously, except for those of Group 3 that hibernated in various sites for prolonged times. However, two bats tracked late in autumn did make a few brief pauses out in the open during a few nights (night-roosting?), but this was included as part of their active time because the sum of these pauses were insignificant compared to the total time spent outside roost.

Bats of Group 1 and 2 were all adult females, whereas bats of Group 3 were juvenile females plus one adult male (Table 1). The bats of Group 3 also hibernated during parts of the study period (Table 1), i.e. they stayed in a site (unheated house, barn, cliff) other than the roost in which they were captured. However, when ambient temperatures later increased, they all left hibernation, returned to the roost and resumed hunting (hibernation periods were not included in active time out of roost). One juvenile (Bat 074) apparently left the roost permanently just three nights after it was tagged; prior to leaving, it had expanded its range greatly (included in Fig. 1, but not in any calculations). The last relocation was made about 8 km from the roost. The bat with the smallest range (Bat 130a of Group 1) left the roost after it was tagged, and roosted in a large pine tree 600 m from the roost house. Another female (Bat 066) moved to a different house after it was tagged (800 m away), but lost the tag the following day.

The number of active periods increased from Group 1 to 2, but did not increase further in Group 3 (i.e. two active periods implies one roost visitation during the night). However, the duration of visits increased in Group 3 (Table 2), i.e. the bats of Group 3 had longer but not more frequent visits. A maximum of five visits were made in one night. When estimated as a percentage of night length, the duration of roost visits was highest in Group 1 and smallest in Group 3 (54.1 vs. 16.4 %). Body mass was negatively related to the average number of active periods ($z=3.30$, $p=0.001$) and to the duration of roost visits ($z=2.83$, $p=0.005$).

Weather conditions generally worsened during the autumn, with lower temperatures (Table 2) and more precipitation. Average time active was negatively related to temperature at both exit and return ($z=3.30$ and 3.05, respectively, $p<0.01$). Likewise, roost visits were negatively related to temperature at exit and return ($z=2.79$ and 2.86, respectively, $p<0.01$). At exit, maximum and minimum temperatures were 19.0 and 0.5 °C, respectively (Fig. 6). At return, maximum and minimum temperatures were 16.0 and -2.0 °C, respectively. The minimum temperature when a bat was hibernating was -5.5 °C. Among 14 bats, the mean temperature at exit exceeded 10.0 °C for eight individuals and at return for six individuals. The overall averages were 9.8±3.9 °C at exit ($n=138$ individual nights) and 8.0±4.2 °C at return ($n=124$).

Radio-tracked bats were active at light intensities below approximately 1700 lux (Fig. 5), intensities that decreased from Group 1 to Group 3 (Table 2). Bats of Group 2 entered the roost under significantly darker conditions than they emerged in ($z=3.41$, $p=0.001$), but no such difference was found in Groups 1 and 3. Using individual bat nights, light levels at exit were significantly higher than at return ($z=2.79$, $p=0.05$, $n=122$), but the difference between the means was only 38.8 lux. Bats of Group 1 had about an equal number of individual nights with light levels higher at exit than at return. Bats of Group 2 had a large majority of individual nights with light levels at exit higher than at return, while for bats of Group 3, the levels were identical in most cases (i.e. zero or close to zero). One bat of Group 1 (Bat 158a) deviated considerably, returning to the roost in much brighter conditions than leaving (but showing a large standard deviation), i.e. it shifted its active period to later in the night. No bat was ever recorded as active (out of roost) in daylight.

Discussion

On bright nights bats are supposedly at much higher risk from predators, but may not be able to afford to postpone foraging. A short foraging season and the demands of reproduction should only intensify this conflict between predator avoidance and food collection. Northern bats in this study were living at the northern edge of the species' distribution. In fact, it is the northernmost population of any species of bat in the world (Rydell et al. 1994). Living well above the Arctic Circle, one might expect that the light summer nights with the sun above the horizon would represent a special challenge for these bats. As indicated in this study, the bats' activity at this time was limited to only a short period during the darkest part of the night and within a small home range. This is the time of pregnancy and partly the lactating period, when their energy needs are at maximum. It is, however, possible that not all the bats used in this study were breeding, because not all adults breed every year. Later in summer, as the sun dropped increasingly below the horizon at night, the bats increased greatly the length of their active period, their flight lengths and home range. All measures of bat activity and range correlated with night length, even though during the first period the bats did not experience darkness and during the last period the bats did not use the full length of the night (sensu Erkert 1978; Rydell et al. 1996). In Troms, it is likely that the effects of light substantially overweighed the effects of reproduction, and that the most important factor limiting activity early in the foraging season was risk of predation.

Increase in activity and home range was also associated with the first flight of the young (sensu Catto et al. 1995). De Jong (1994) found that home range size of northern bats increased during the summer, from small ranges (0.11-0.23 km^2) during May and June, to 1.33 km^2 in July and 7.57 km^2 in August. Foraging time also increased from about 1 to 3.4 hours in the same period. Insect abundance decreased from June through July, but showed a small increase in August, and was correlated with hunting activity of bats. De Jong (1994) concluded that the increase in activity followed parturition (as a general pattern) and that the increase in range coincided with the flight of juveniles the first study year, but was earlier in the second year due to a lower abundance of insects (sensu Rydell 1989).

Similarly, O'Donnell (2001) suggested that the range expansion of post-lactating female long-tailed bats coincided with juveniles beginning to fly and was possibly unrelated to food availability. The first volant young in Troms have been observed at the end of July, but more regularly after 10 August. It is thus evident that adult females managed to get enough energy and nutrients both for themselves and their offspring during only a short hunting burst, indicating an adequate abundance of insects during this period. Increased activity and range may have been partly associated with a decrease in insect abundance, but also with a reduced need to return to roosts during the night and a need to feed more to build up fat layers prior to hibernation (Henry et al. 2002; Lucan and Radil 2010). It seems unlikely that insect abundance dropped dramatically at the beginning of August, so the increase in foraging time may not be fully explained by a reduced abundance of prey (sensu Rydell 1986, 1993; de Jong 1994; Hickey and Fenton 1996; Rydell et al. 1996; Speakman et al. 2000; Ciechanowski et al. 2007). Although the number of individuals in this study was not large and further studies are needed, the overall trends were clear.

Although bats experience perpetual light in most of July, the nights were still much darker than daylight and these bats appeared to have their tolerance limit at about 1700 lux. It should be noted that although the sun was above the horizon (midnight sun), it dropped behind hills shading the roost houses at night. Shading effects from hills in south Norway and from closed canopy forest in Italy resulted in soprano pipistrelles *Pipistrellus pygmaeus* emerging up to two hours earlier (Michaelsen et al. 2011; Russo et al. 2011b, sensu Degn 1983; Catto et al. 1995). Canopy cover also affected emergence time in the barbastelle *Barbastella barbastellus* in Italy (Russo et al. 2007). Likewise, overcast skies may have enabled bats in Troms to leave the roost earlier and hunt longer. Under a clear sky, night temperatures often dropped significantly, although temperature inversions may provide bats with slightly higher temperatures higher up the hill. However, it is still remarkable that these bats hunted regularly in temperatures well below 10 °C (sensu Rydell 1989; Catto et al. 1995; Ciechanowski et al. 2007, Wojciechowski et al. 2007). The greatest increase in range and activity was associated with the end of the bats' yearly active period, when some may already have entered annual hibernation (Frafjord 2007). Some of the longer flights at this time could have been both hunting and "exploratory", perhaps searching for a suitable site in which to hibernate, the latter being needed more by inexperienced young than by adults (sensu de Jong 1994; Catto et al. 1996).

The five predictions made for this study were based on published studies from much further south, where nights are dark and the demands of reproduction are, at least in some studies, thought to be the major factor regulating bat activity. None of the predictions were entirely fulfilled as it appeared that night length had a profound influence on the northern bat's activity and range. The limited activity and range under midnight sun most likely resulted from predation risk and the later increase was closely associated with night length until the night was sufficiently long and, to a large extent, with volant young. This increase occurred before a significant reduction in insect abundance could be expected. Consequently, prediction 1) was falsified as home range size increased throughout the foraging season, possibly stepwise. The first part of prediction 2) was supported, but not the last part as home range size was as much affected by night length as activity. Activity did not peak in early August and prediction 3) was falsified. Prediction 4) was partly supported, because although the duration of nightly visits to roosts increased throughout the season, it decreased relative to length of night being relatively much higher in July. Lower ambient temperatures (above zero) were not associated with reduced activity or range and prediction 5) was falsified.

Acknowledgments

Thanks to Ole Jakob Løvhaug and Ola and Svanhild Tune for their hospitality and for permitting me to work on their estates (at night!), and thus making this study possible. I also thank John D. C. Linnell and John Odden at the Norwegian Institute for Nature Research for lending me a receiver when my own collapsed. Permission to trap and tag bats was granted by the Norwegian Directorate for Nature Management. Rob Barrett corrected style and spelling and two reviewers provided helpful suggestions to the manuscript.

References

Altringham, J .D. 2011. Bats: from evolution to conservation. Oxford University Press, Oxford.

Barclay, R.M.R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behav. Ecol. Sociobiol. 24, 31-37.

Boyles, J.G., Dunbar, M.B., Storm, J.J., Brack, V. 2007. Energy availability influences microclimate selection of hibernating bats. J. Exp. Biol. 210, 4345-4350.

Catto, C.M.C., Hutson, A.M., Racey, P.A., Stephenson, P.J. 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. J. Zool., Lond. 238, 623-633.

Catto, C.M.C., Racey, P.A., Stephenson, P.J. 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. J. Zool., Lond. 235, 635-344.

Ciechanowski, M., Zajac, T., Bilas, A., Dunajaski, R. 2007. Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. Can. J. Zool. 85, 1249-1263.

Degn, H.J. 1983. Field activity of a colony of serotine bats (*Eptesicus serotinus*). Nyctalus (N.F.), Berlin 1, 521-530.

De Jong, J. 1994. Habitat use, home-range and activity pattern of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. Mammalia 58, 435-548.

Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D. 2000. Functional significance of emergence timing in bats. Ecography 23,32-40.

Erkert, H.G. 1978. Sunset-related timing of flight activity in Neotropical bats. Oecologia 37, 59-67.

Fenton, M.B., Rautenbach, I.L., Smith, S.E., Swanepoel, C.M., Grosell, J., Jaarsveld, J.V. 1994. Raptors and bats: threats and opportunities. Anim. Behav. 48, 9-18.

Frafjord, K. 2001. Distribution of the northern bat *Eptesicus nilssonii* above the Arctic Circle in Norway (in Norwegian, summary in English). Fauna 54, 124-131.

Frafjord, K. 2007. Possible hibernation sites of the northern bat *Eptesicus nilssonii* at its northern range limit in Norway (in Norwegian, summary in English). Fauna 60, 246-254.

Halle, S., Stenseth, N.C. (Eds.). 2000. Activity patterns of small mammals: an ecological approach. Ecological studies, Vol. 141, Springer, Berlin.

Henry, M., Thomas, D.W., Vaudry, R., Carrier, M. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). J. Mammal. 83, 767-774.

Hickey, M.B.C., Fenton, M.B. 1996. Behavioural and thermoregulatory responses of female hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey availability. Ecoscience 3, 414-422.

Jones, G., Rydell, J. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Phil. Trans. Royal Soc. Lond. B 346, 445-455.

Lawson, E.J.G., Rodgers, A.R. 1997. Differences in home-range size computed in commonly used software programs. Wildl. Soc. Bull. 25, 721-729.

Lucan, R.L., Radil, J. 2010. Variability of foraging and roosting activities in adult females of Daubenton's bat (*Myotis daubentonii*) in different seasons. Biologia 65, 1072-1080.

Michaelsen, T.C., Jensen, K.H., Högstedt, G. 2011. Topography is a limiting distributional factor in the soprano pipistrelle at its latitudinal extreme. Mamm. Biol. 76, 295-301.

O'Donnell, C.F.J. 2001. Home range and use of space by *Chalinolobus tuberculatus*, a temperate rainforest bat from New Zealand. J. Zool., Lond. 253, 253-364.

Parker, D.I., Lawhead, B.E., Cook, J.A. 1997, Distributional limits of bats in Alaska. Arctic 50, 256-265.

Racey, P.A., Speakman, J.R. 1987. The energy costs of pregnancy and lactation in heterothermic bats. Symp. Zool. Soc. Lond. 57, 107-125.

Russo, D., Cistrone, L., Garonna, A.P., Jones, G. 2011b. The early bat catches the fly: daylight foraging in soprano pipistrelles. Mamm. Biol. 76, 87-89.

Russo, D., Cistrone, L., Jones, G. 2007. Emergence time in forest bats: the influence of canopy closure. Acta Oecol. 31, 119-126.

Russo, D., Maglio, G., Rainho, A., Meyer, C.F.J., Palmeirim, J.M. 2011a. Out of the dark: diurnal activity in the bat *Hipposideros ruber* on São Tomé island (West Africa). Mamm. Biol. 76, 701-708.

Rydell, J. 1986. Foraging and diet of the northern bat *Eptesicus nilssoni* in Sweden. Holarctic Ecol. 9, 272-276.

Rydell, J. 1989. Feeding activity of the northern bat *Eptesicus nilssoni* during pregnancy and lactation. Oecologia 80, 562-565.

Rydell, J. 1992. Occurrence of bats in northernmost Sweden (65°N) and their feeding ecology in summer. J. Zool., Lond. 227, 517-529.

Rydell, J. 1993. Variation in foraging activity of an aerial insectivorous bat during reproduction. J. Mammal. 74, 503-509.

Rydell, J., Entwistle, A., Racey, P.A. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76, 243-252.

Rydell, J., Speakman, J.R. 1995. Evolution of nocturnality in bats: Potential competitors and predators during their early history. Biol. J. Linn. Soc. 54, 183-191.

Rydell, J., Strann, K.-B., Speakman, J.R. 1994. First record of breeding bats above the Arctic Circle: northern bats at 68-70°N in Norway. J. Zool., Lond. 233, 335-339.

Siivonen, Y., Wermundsen, T. 2008. Distribution and foraging habitats of bats in northern Finland: *Myotis daubentonii* occurs north of the Arctic Circle. Verspertilio 12, 41-48.

Speakman, J.R. 2001. The evolution of flight and echolocation in bats: another leap in the dark. Mamm. Rev. 31, 111-130.

Speakman, J.R., Bullock, D.J., Eales, L.A., Racey, P.A. 1992. A problem defining temporal pattern in animal behaviour: clustering in the emergence behaviour of bats from maternity roosts. Anim. Behav. 43, 491-500.

Speakman, J.R., Hays, G.C., Webb, P.I. 1994. Is hyperthermia a constraint on the diurnal activity of bats? J. Theor. Biol. 171, 325-339.

Speakman, J.R., Rydell, J., Webb, P.I., Hayes, J.P., Hays, G.C., Hulbert, I.A.R., McDevitt, R.M. 2000. Activity patterns of insectivorous bats and birds in northern Scandinavia (69 °N). Oikos 88, 75-86.

Speakman, J.R., Thomas, D.W. 2003. Physiological ecology and energetics of bats. In: Kunz, T.H., Fenton, M.B., (Eds.), Bat ecology. The University of Chicago Press, Chicago, pp. 430-490.

Wilkinson, L.C., Barclay, R.M.R. 1997. Differences in the foraging behaviour of male and female big brown bats (*Eptesicus fuscus*) during the reproductive period. Ecoscience 4, 279-285.

Wojciechowski, M.S., Jefimow, M., Tegowska, E. 2007. Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). Comp. Bioch. Physiol., Part A 147, 828-840.

Figure legends:

Fig. 1. Individual home ranges (MCP) of northern bats: a) Roost 1, temporal Group 1 (July) and 2 (August), b) Roost 2, Group 1 and 2, c) Roost 1 and 2, Group 3 (September-October; note different scale). The range of Bat 045 has been included in both a) and c) for direct comparison (marked with *). The approximate locations of the two roosts are indicated by 1 and 2.

Fig. 2. Home range size (km^2) of northern bats relative to length of night (hours, circles) and average time out (hours, triangles). R^2 with length of night=0.79 (quadratic r^2=0.86, finely dotted line), with average time out =0.71, p<0.001 for all.

Fig. 3. Active period of northern bats in terms of both average number of hours out of roost (circles) and number of periods out of roost (triangles) relative to length of night. R^2 linear with hours=0.91, p<0.001, with numbers=0.39, p=0.011.

Fig. 4. Maximum time (hours) northern bats spent out of their roosts throughout the season in relation to sunset and sunrise. The bars represent individual bats and are only artificially centred around zero (introduces only marginal error).The y-axis represents hours before (-) and after (+) the time when the sun is at its lowest at this latitude (zero).

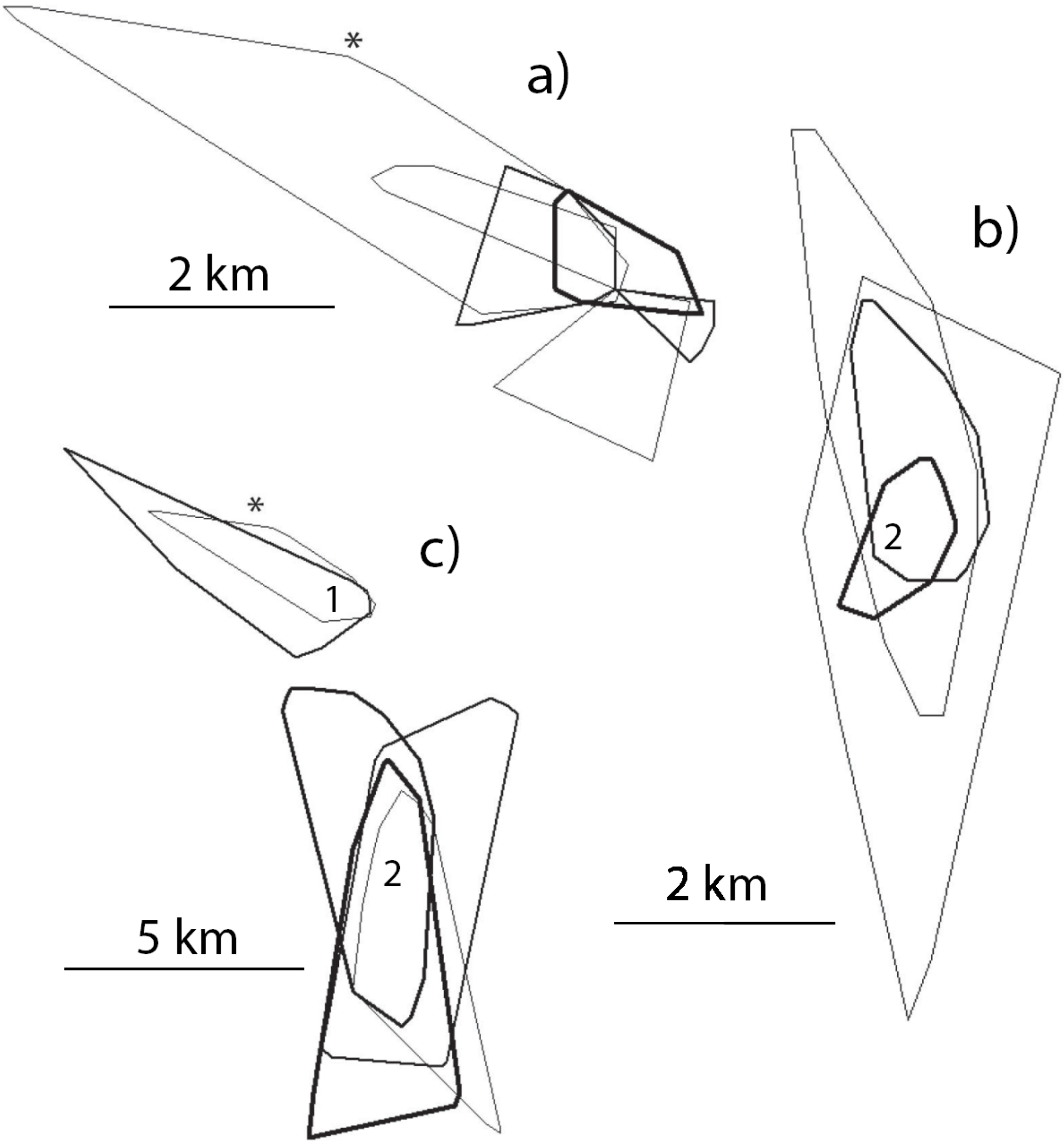
Fig. 5. Light intensity (lux) at exit plotted against light intensity at return for individual bat nights (r=0.72, p<0.001, n=122).

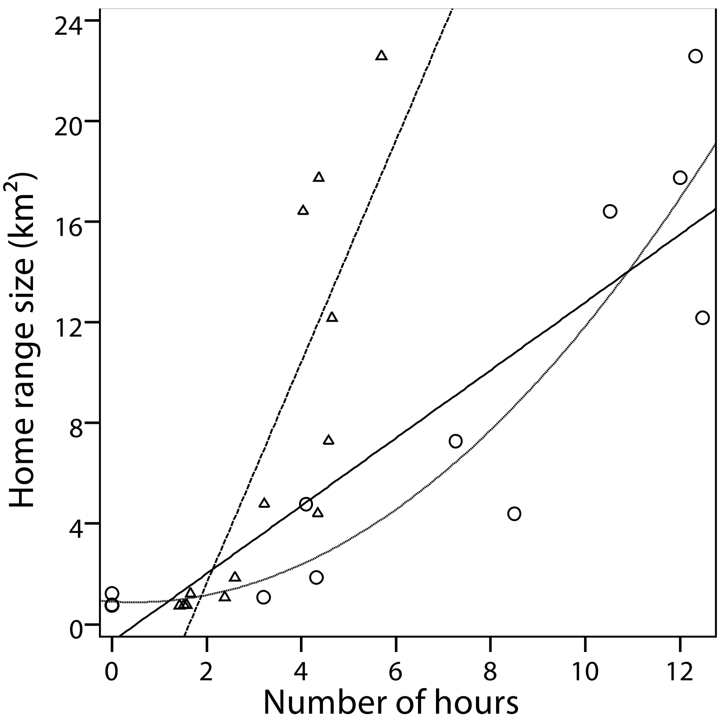
Table 1. Study periods of individual northern bats and their home range size in Troms, Norway (figures in brackets were included in some illustrations, but not in statistical tests). Hours tracked is the number hours the bats were tracked when active and flying. Included are also the numbers of nights they were active and tracked, numbers of nights they were hibernating, and partitioning into three temporal groups. DD = data deficient, i.e., the bat was tracked, but not enough data was collected. Date format: day.month.year.

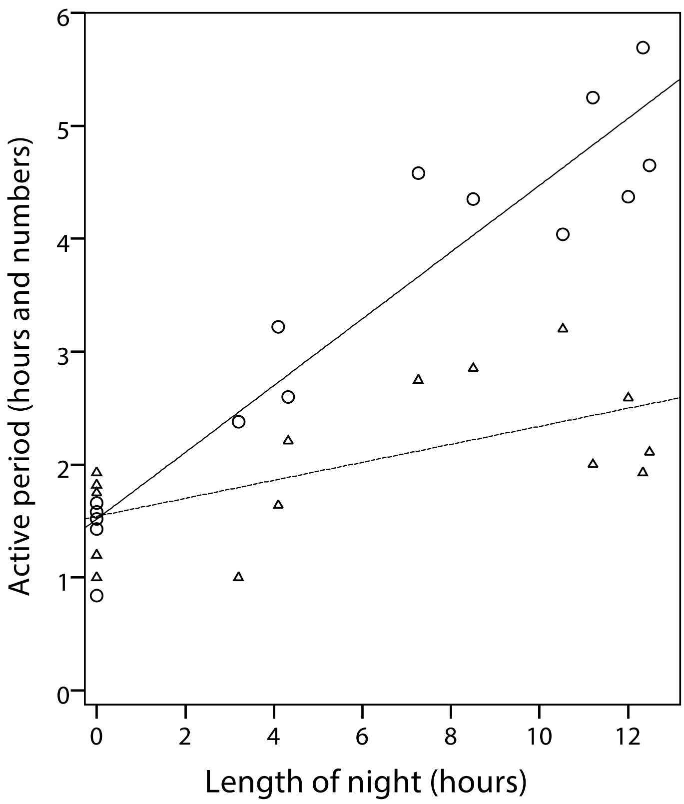
Roost	Bat	Age	Period tracked	Median date	Range (km^2)	Hours tracked	Nights active	Hiber-nating	Group
1	130a	Adult	1-7.7.2003	4.7	[0.24]	4.4	4 + 2DD	1?DD	[1]
1	066	Adult	9-10.7.2003	-	-	1.2	1DD	0	[1]
1	100	Adult	23-28.7.2003	26.7	1.22	8.3	5	0	1
1	123	Adult	1-4.8.2003	2.8	1.07	7.7	3 + 1DD	0	1
1	045	Adult	1-11.8.2003	6.8	4.78	35.4	11	0	2
1	041	Adult	5-17.7.2004	11.7	0.74	15.7	11	0	1
1	008	Adult	21-27.7.2004	24.7	0.77	10.7	7	0	1
2	130b	Adult	31.7-15.8.2004	7.8	1.86	41.4	14 + 1DD	0	2
2	109	Adult	12-25.8.2004	18.8	7.28	51.5	12 + 1DD	0	2
1	074	Juvenile	26-29.8.2004	[28.8]	[9.62]	11.3	2 + 2DD	0	[3]
2	053	Adult ♂	8-22.9.2004	15.9	16.42	39.6	10	4 + 1DD	3
2	020	Juvenile	23-26.9.2004	-	-	6.5	3DD	?	[3]
2	158a	Adult	12-21.7.2005	16.7	0.76	14.5	9	0	1
2	087	Adult	22.8-5.9.2005	29.8	4.40	54.9	13	0	2
2	158b	Juvenile	10.9-5.10.2005	21.9	17.75	73.4	17 + 1DD	6 + 1DD	3
2	142	Juvenile	19.9-12.10.2005	30.9	22.58	80.5	14	6 + 2DD	3
2	106	Juvenile	14.9-14.10.2006	29.9	12.18	42.0	11	10	3

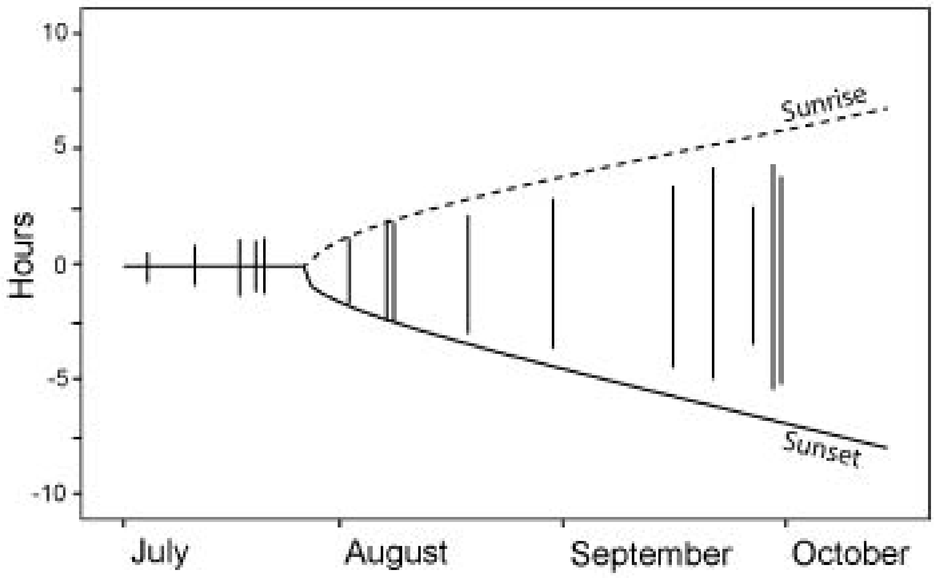
Table 2. Mean±SD of 13 measured parameters for three temporal groups of northern bats (Group 1= July, Group 2 = August, and Group 3 = September-October), with the number of bats in each group. Time is given in hours (h) or minutes (m). ANOVA-tests between groups.

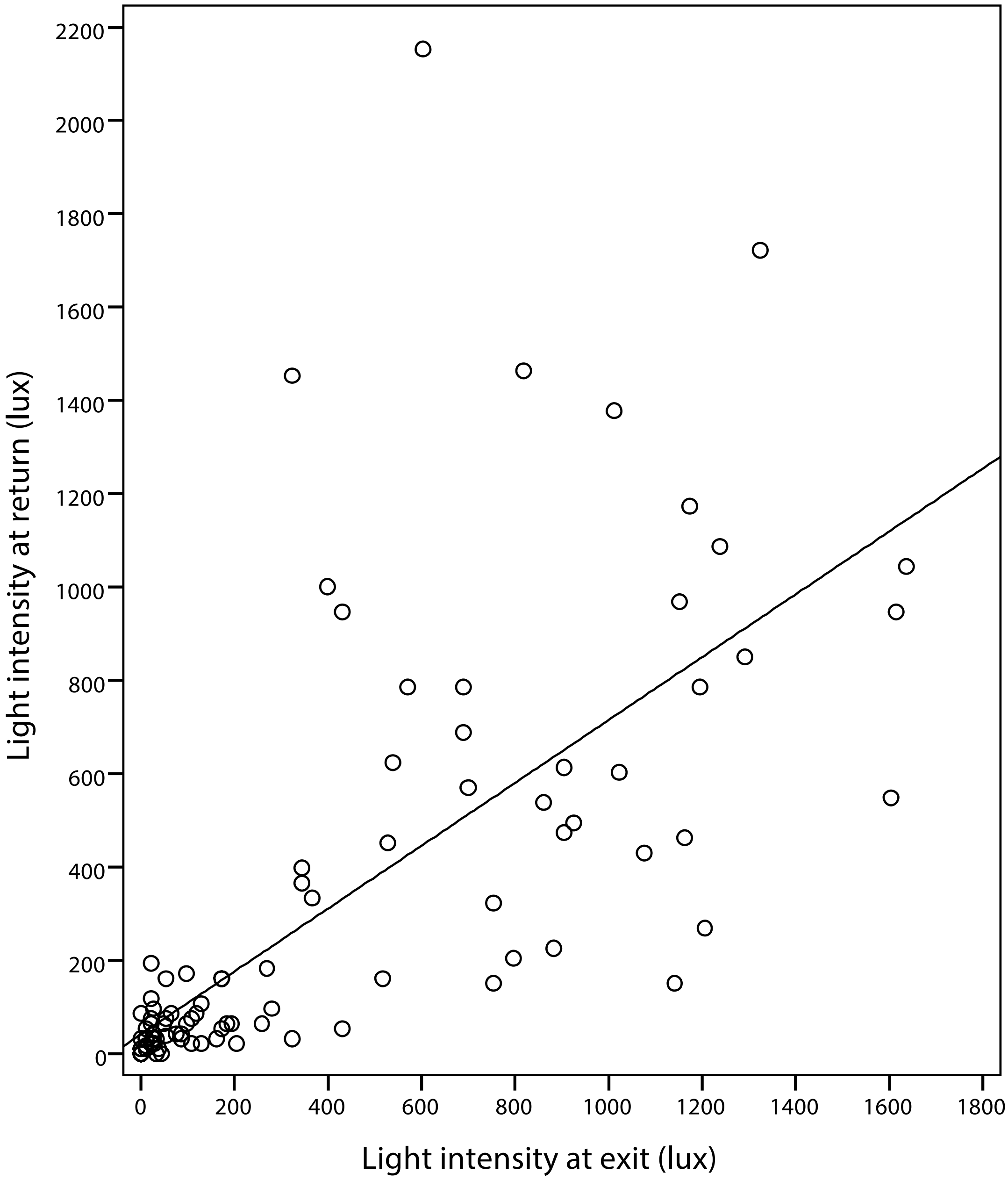
	Group 1	Group 2	Group 3	F	d.f.	p<
Home range size (km^2)	0.91±0.22	4.58±2.22	17.23±4.28	44.8	2, 10	0.001
Max. diameter (km)	1.21±0.38	4.43±1.67	7.88±1.48	49.8	2, 14	0.001
Average time out (h)	1.57±0.49	3.69±0.94	4.80±0.67	31.7	2, 12	0.001
Max. time out (h)	2.23±0.60	5.29±1.06	8.75±1.73	40.6	2, 12	0.001
Average # of active periods	1.45±0.43	2.36±0.56	2.37±0.53	6.0	2, 12	0.05
Max. # of active periods	2.00±0.89	3.75±0.50	4.40±1.82	5.7	2, 12	0.05
Duration of roost visits (m)	17.2±21.1	76.3±47.3	108.5±18.5	11.9	2, 11	0.05
Temp. at exit (°C)	12.5±2.4	11.6±3.1	6.8±2.5	36.2	2, 11	0.001
Temp. at return (°C)	11.1±2.1	8.2±4.3	6.3±3.9	13.6	2, 11	0.001
Lux at exit	789.0±460.7	291.7±353.1	48.4±48.4	11.4	2, 11	0.01
Lux at return	808.4±503.8	167.9±203.5	34.5±30.1	21.5	2, 11	0.001
Length of night (h)	0.53±1.31	6.05±2.18	11.70±0.83	80.1	2, 12	0.001
Body mass (g)	9.9±2.3	10.8±0.6	8.9±1.0	1.59	1, 13	n.s.
Number of bats	5-7	4	4-6			


a)
*
2 km
b)
2
2 km
c)
*
1
2
5 km


Home range size (km²)
0
4
8
12
16
20
24
0
2
4
6
8
10
12
Number of hours


Active period (hours and numbers)
0
1
2
3
4
5
6
0
2
4
6
8
10
12
Length of night (hours)


10
5
0
-5
-10
Hours
Sunrise
Sunset
July
August
September
October



Light intensity at return (lux)
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
0
200
400
600
800
1000
1200
1400
1600
1800
Light intensity at exit (lux)

515