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Roost selection, activity and dispersal of Leisler's bat, *Nyctalus leisleri* (Kuhl, 1818) during the pre-hibernal and hibernal periods

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Introduction

The majority of a bat's life is spent in roosts, so roost selection is likely an important factor affecting survival. Throughout the year, roost selection depends on the diversity and abundance of roosts, the distribution and abundance of food, and an energy economy influenced by body size and the physical environment (Kunz and Lumsden 2003). During hibernation, however, choosing an optimal roost site is fundamental to maintaining energy balance (McNab 1982). Hibernacula requirements vary among bat species. For example, *Myotis lucifugus* requires stable temperatures above freezing and high humidity (McManus 1974), but *Eptesicus fuscus* can tolerate temperatures below freezing in sites with low humidity (Beer and Richards 1956). In many temperate bat species, it is common to observe migration, often over large distances, to locate suitable winter hibernation sites (Hutterer *et al.* 2005).

Leisler's bat, *Nyctalus leisleri*, (Kuhl, 1818) (Figure 1) has been recorded over much of the Palaearctic but is poorly documented outside Europe (Dietz *et al.* 2009). Throughout most of its range, it is considered rare except for Ireland where it is common (Stebbing and Griffith 1986; O'Sullivan 1994). In continental Europe, Leisler's bats are known to migrate over large distances between hibernation and summer roosting sites (Schober and Grimmberger, 1999). For example, individuals ringed in Russia have been recovered in Turkey (1245km) (Likhachev, 1980; Panyutin, 1980); an individual tagged in Italy was recovered in Poland, a straight line distance of 960km (Dondini *et al.* 2012); and one bat ringed in Germany was recaptured in Spain, a distance of 1567km (Ohlendorf *et al.*, 2000). Summer or maternity roost sites have been recorded in woodpecker holes or other tree holes, often in beech and oak, as well as in buildings and bat boxes. Similarly hibernation roosts have been found in trees holes and in buildings (Ruczyński & Bogdanowicz 2005; Spada *et al.* 2008). There is currently no evidence that any Irish bat species migrate to hibernation sites either within or outside the island (Hutterer *et al.* 2005). Furthermore, no hibernation sites comparable to the large cave hibernacula in continental Europe have been identified for any Vespertilionid in Ireland (McAney, 2006). Given its temperate oceanic climate, with mean summer temperatures ranging between 15 – 20°C, and winter temperatures 4.0 - 7.6°C (Source: Met Éireann), Ireland may provide suitable year-round conditions for temperate bat species. Summer roost sites in Ireland have been reported primarily in buildings (Shiel & Fairley 1999, Waters *et al.* 1999, McAney 2006), with only a few tree roosts identified (mainly oak and ash; Fairley, 2001). Activity and dispersal of *N. leisleri* during the summer months has been examined in previous studies (Shiel and Fairley 1998; Shiel *et al.* 1999; Russ *et al.* 2003). However, little is known about activity patterns of Leisler's bats in Ireland leading up to, and during, hibernation. An understanding of the behaviour and specific climatic and roosting requirements before and during hibernation is essential for effective conservation and management of these species throughout their lifecycle.

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Figure 1. Leisler's bat on a tree © Austin Hopkirk

We radio-tracked adult male and female *N. leisleri* in Northern Ireland to examine activity, roost selection and dispersal during the pre-hibernal and hibernal periods. More specifically we tested the hypotheses that i) periods of torpor increase with decreasing temperature; ii) Irish populations do not make long-distance migrations to hibernation sites; iii) and roost selection will change during the pre-hibernal and hibernal periods.

Materials and Methods

Fieldwork was carried out in Northern Ireland from 29th July 2002 to 12th November 2002 and from 23rd August 2003 to 21st January 2004. Bats were captured at two sites throughout the study period. In July and early August, females were captured at a maternity roost (>100 individuals) in the attic of an occupied urban building (J 34771 72068), while from August through to October male and female bats were captured at a mixed, predominantly coniferous woodland site containing occupied bat boxes, some 40.32km south of the initial maternity roost (Tollymore Forest Park; J 3938 31898) (e.g. Figure 2).

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Figure 2. Leisler bats in a bat box © Austin Hopkirk

Tagging and Tracking

Bats were captured on multiple occasions in both years (see Appendix 1). Between 5 to 8 individual bats were tagged at one time. All bats were caught in hand nets at evening emergence. Bat boxes were first inspected by day using an endoscope to minimise disturbance. Individuals were identified to species and sex, and weight (g) and forearm length (mm) were determined (see Appendix 1). Transmitters were no more than 5% of the bat's body weight (Aldridge & Brigham 1988). For tagged individuals, the interscapular fur was trimmed close to the skin and temperature-sensitive transmitters (Holohil Systems Ltd., Ontario) were attached using Skinbond surgical cement (Smith and Nephew, Largo, Florida, USA).

Transmitter signals were received by a pair of Yagi antennae and Mariner 57 receiving sets (Mariner Radar, Lowestoft, UK). Tagged bats were radio-tracked at night using the close follow approach by vehicle with a team of 2-3 people using a Yagi antenna mounted on a 3-metre long mast through the sunroof. A handheld Yagi antenna was used when on foot. Up to 4 bats were tracked at once in the summer months and as many as 8 at one time once the bats were less active towards November. Measurements of signal direction ($^{\circ}$), ambient temperature, and skin temperature were recorded every ten minutes throughout the night, with a break approximately between 01:00 and 03:00 hrs. In previous studies, skin temperature has been shown to accurately reflect body temperature (e.g. Willis and Brigham 2003). Using skin temperature as well as activity (static or moving signal), bat behaviour was classified as either 'roosting' or 'in-flight'. At skin temperatures below 6 $^{\circ}$ C, bats were considered to be in torpor, following modal temperature for hibernation for Vespertilionids (Webb *et al.* 1996). Throughout July, August and September, no more than four individual bats were tracked simultaneously. As roost excursions diminished in

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frequency and duration later in the study, it became possible to monitor eight tagged bats simultaneously.

Roost Characteristics

Roosts identified from radio-tracking were visited in the day and were classified as domicile (human-inhabited buildings), non-domicile (uninhabited buildings), bat box and trees. For all tree roosts, distance to the nearest habitat edge, the type of cavity (exfoliating bark, rot hole and split) was recorded as well as the tree girth and species.

Data Analysis

Data were analysed using Minitab v13 statistical software (Ryan and Joiner 1994) and R (R Core Team 2012) with the Forecast package (Hyndman *et al.* 2012). To limit the effects of non-independence of data points collected from the same individual means were taken. Nightly means were taken from measurements per individual taken on average between 10 pm and 7 am. A Wilcoxon test was used to test differences between nightly mean skin and ambient temperature for individual bats across the season in both 2002 and 2003. Mixed effect models controlling for the individual were unsuitable as q-q plots showed residuals to be non-normal. ANOVA was used to test for differences between ambient temperature during periods of flight and roosting. A Wilcoxon test was used to test for differences between skin temperature of bats in flight and roost as q-q plots showed ANOVA residuals to be non-normal.

The mean of the roosting and flight encounters per quarter bat per bat was calculated as an index of activity (i.e. roosting versus flight).

Time series analysis using ARIMA models (e.g. Jia *et al.* 2010), so that temporal non-independence of data was accounted for, was used to examine skin temperature across season for roosting bats, pooled by date and modelled separately in 2002 and 2003. In time-series analyses the next value in the time series is dictated by autoregressive terms, moving average terms and deterministic trend terms as well as using unlagged ambient temperature as a further predictor variable. The coefficients for these terms are given with their standard errors. ARIMA models were selected using AICc. The inclusion of a trend term is evidence of a temporal trend that is not explained by an auto-correlated decrease in temperature. The inclusion of an ambient temperature term implies that there is an association between ambient temperature and skin temperature.

Results

In total, 29 adult *N. leisleri* were tagged with radio transmitters and 25 tracked on 94 nights in 2002 (29th July to 12th November; 5 males, 9 females) and 101 nights in 2003 (2 males, 9 females; 23rd August to 31st December) (see Appendix 1). The mean forearm lengths for tagged bats, with standard errors, were 43.18 ± 0.27 mm for males and 43.71 ± 0.28 mm for females and the mean masses were 17.0 ± 0.57 g for males and 18.38 ± 0.55 g for females. Over the entire study period, bats were tagged from a total of eight roosts (one maternity site, and seven bat boxes) and tracked to a further 68 roosts.

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Seasonal activity patterns

Seasonal variation in skin and ambient temperature for individual bats in both 2002 and 2003 were highly correlated (2002: Spearman's Rank Correlation Coefficient = 0.638, $p < 0.001$; 2003: Spearman's Rank Correlation Coefficient = 0.600, $p < 0.001$ (means per bat per day)). Overall, there was a significant difference in skin temperature between bats in flight (30.39 ± 1.35 °C) and those in the roost (18.86 ± 0.83 °C) (Wilcoxon: $W = 220$, $N=1070$, $p < 0.001$). Ambient temperature was significantly higher during the time when bats were in flight (12.92 ± 0.52 °C) than when they were in the roost (11.49 ± 0.37 °C) (ANOVA: $F_{1, 43} = 4.58$, $p = 0.038$).

From August to November, time spent in flight decreased while time spent roosting increased (Figure 3). In the second quarter of August, bats were observed roosting about 50% of the time. However, time spent roosting increased from August to October and during mid-November bats were observed roosting 100% of the time. This is in contrast with the ambient temperature which gradually decreased over this period. The best ARIMA model of skin temperature for 2002 included an ambient temperature term (0.58 ± 0.28), a deterministic decline (-0.41 ± 0.10) and a moving average term (-0.87 ± 0.11). For skin temperatures in 2003, the best model includes an ambient temperature term (0.78 ± 0.11), a deterministic decline (-0.17 ± 0.11), an autoregression term (-0.42 ± 0.14) and a moving average term (-0.55 ± 0.14). Over the study period, ambient temperature gradually decreased from about 13.5 °C in mid-September to about 6 °C in late December (Figure 4). The skin temperature of roosting bats decreased rapidly from about 29.5 °C in the second half of September to about 15 °C in the second half of October. After this period, from the start of November to the end of December, the pattern of variation in skin temperature matched that of ambient temperature. Mean skin temperatures of roosting bats were similar for both males and females from mid-September to mid-November.

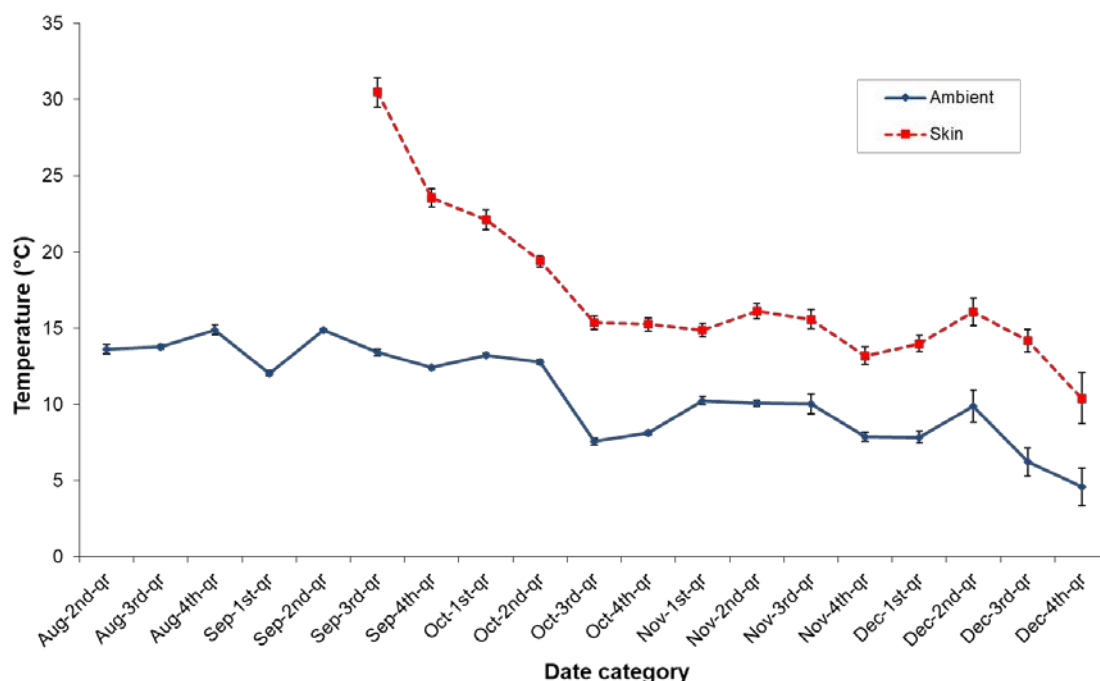


Figure 3. Overall mean skin temperature and mean ambient temperature for radio-tagged bats (N=29) for monthly quarters with an Activity Index (0=100% Roosting, 1=100% Flying). Error bars represent standard errors

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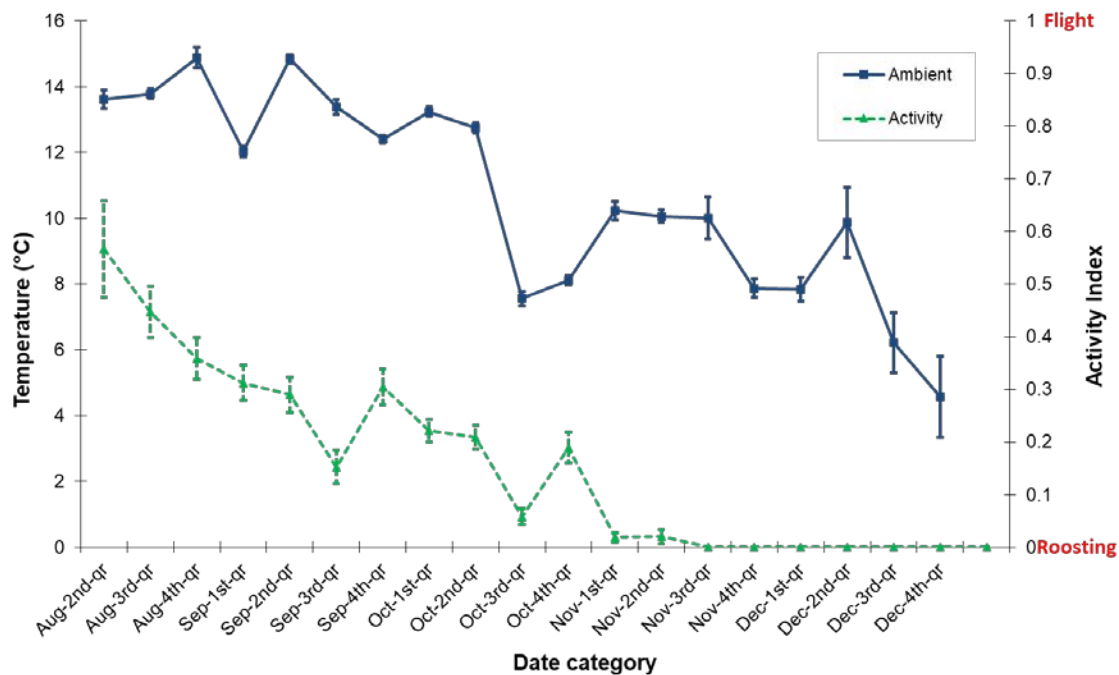


Figure 4. Overall mean skin temperature of roosting bats and mean ambient temperature for radio-tagged bats (N=29) for monthly quarters. Error bars represent standard errors

During September and October, skin temperatures of roosting bats ranged from about 39 °C to 6 °C (Figure 5). During November and December, however, skin temperatures very rarely rose above 24 °C. Below this threshold there is a positive correlation between ambient temperature and skin temperature for September (Spearman's Rank Correlation Coefficient = 0.178, $p < 0.01$), October (Spearman's Rank Correlation Coefficient = 0.473, $p < 0.001$), November (Spearman's Rank Correlation Coefficient = 0.533, $p < 0.001$) and December (Spearman's Rank Correlation Coefficient = 0.685, $p < 0.001$).

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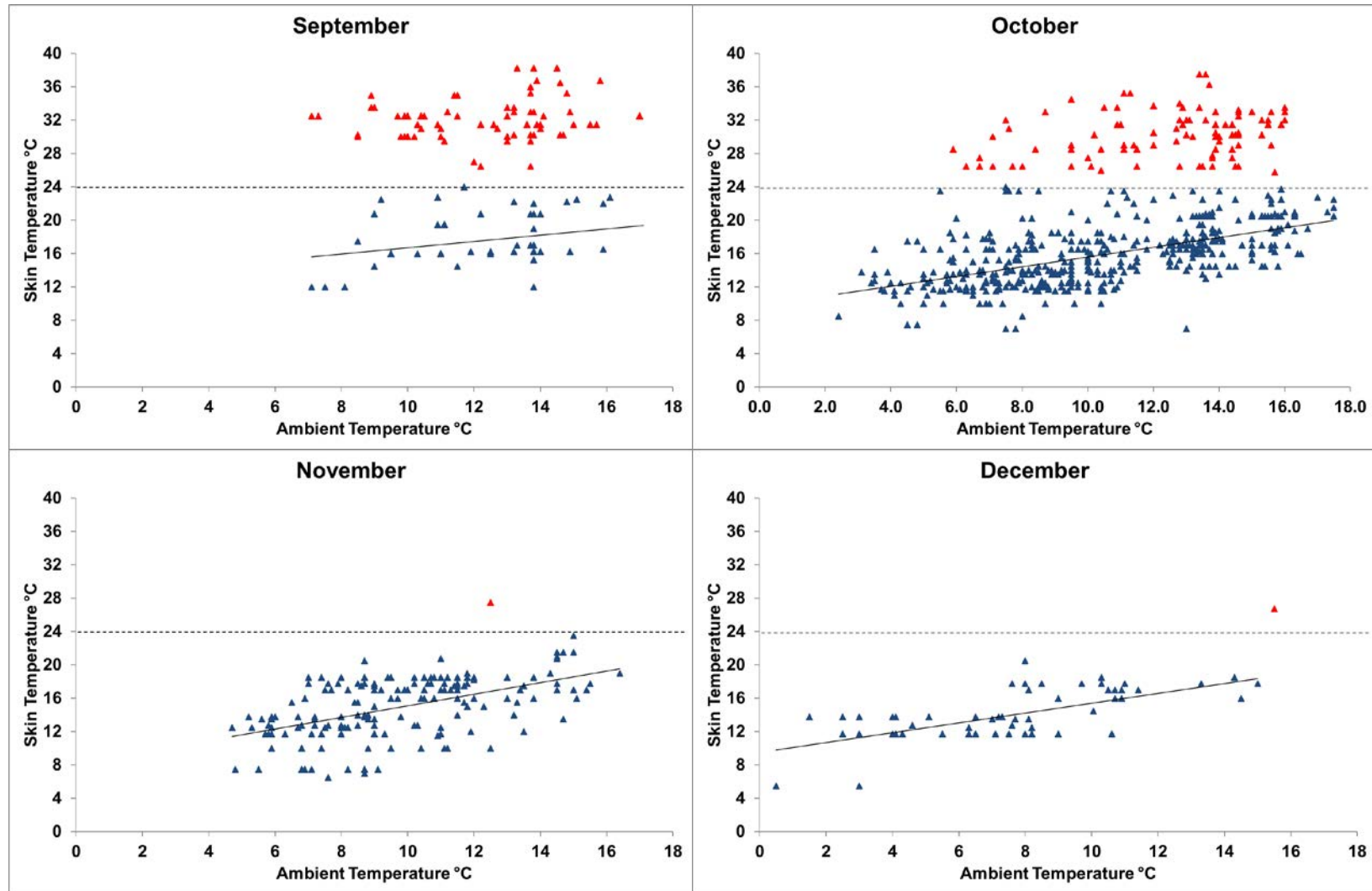


Figure 5. Relationship between ambient temperature and skin temperature of roosting bats for a) September (N=194), b) October (N=587), c) November (N=175) and d) December (N=59). The dotted line represents a maximum roosting skin temperature threshold for November and December with red markers representing temperatures above this threshold and blue markers representing temperatures below). The solid line represents the correlation between ambient and skin temperatures under this threshold.

Dispersal

Across the study period, male Leisler's bats moved a mean distance of 1.41 ± 0.38 km between roosts, while females moved a mean distance of 2.01 ± 0.45 km. The greatest distance travelled was by a female bat that flew 33.81 km at a mean bearing of 184.1° between roosts in a 24 hour period. Distances between successive roosts were greatest during the mid-September to late October period with several movements over 5 km. After mid-October movements between roosts did not exceed 5 km.

Roosts

Bats were recorded using a variety of roost types at the start of the study period. Fifteen roosts were identified in the roof spaces of domiciles; four non-domicile buildings were used, including cracks in walls in barns and an animal byre as well as the roof space of an unoccupied dwelling. Eight bat boxes were used, while 41 tree roosts were identified (Table 1). Generally, bats were recorded in bat boxes and non-domicile buildings from the end of August through to mid-October; trees and, to a lesser extent, domicile buildings from the end of October to mid-November; and just trees after mid-November (Figure 6).

Table 1. Tree species and cavity types used for roosting.

Common name	Latin name	Roost Type				TOTAL
		Exfoliating bark	Rot hole	Split	Unknown	
Ash	<i>Fraxinus excelsior</i>		1			1
Beech	<i>Fagus sylvaticus</i>		6	1	4	11
Birch	<i>Betula pendula</i>		1			1
Elm	<i>Ulmus spp.</i>		1			1
Larch	<i>Larix decidua</i>			1		1
Oak	<i>Quercus spp.</i>	3	3	17		23
Spanish chestnut	<i>Castanea sativa</i>	1				1
Sycamore	<i>Acer pseudoplatanus</i>		2			2
TOTAL		4	14	19	4	41

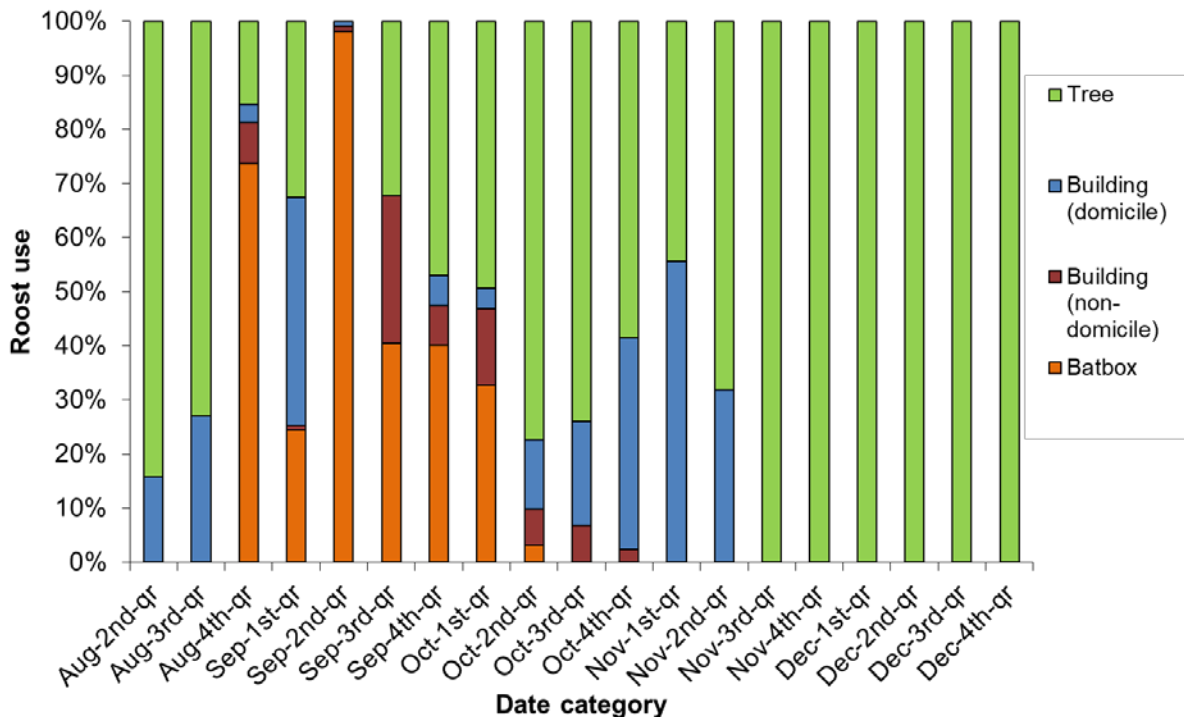


Figure 6. Mean proportion of roost use across month categories

The tree species used most by roosting bats were oak, followed by beech and of the roosts located in trees, the most common type was splits within tree branches (Table 1). Rot holes and exfoliating bark were used to a lesser degree. Eighty-one per cent of roosts in tree splits and 75% of roosts in exfoliating bark roost were located in oaks. In contrast, only 22% of roosts in rot holes were located in oaks with the rest in beech, sycamore, ash and birch. Fifty per cent of identified roosts were on forest edges and paths and 34.5% were within 15m of an edge. The remainder (15.5%) were within 200 m.

Examples of roosts are presented in Figures 7-16.



Figure 7. Maternity roost in an attic in Belfast
© Austin Hopkirk



Figure 8. Wall roost in a crack
© Austin Hopkirk



Figure 9. Roost at a barge board © Austin Hopkirk



Figure 10. Roost under in a hole in a brick wall behind render © Austin Hopkirk



Figure 11. Roost in a rot hole © Austin Hopkirk



Figure 12. Roost in a beech tree © Austin Hopkirk



Figure 13. Roost in an oak tree © Austin Hopkirk



Figure 14. Leisler's bat droppings in a tree roost © Austin Hopkirk



Figure 15. Roost in a split in an oak © Austin Hopkirk



Figure 16. Roost in a oak © Austin Hopkirk

Discussion

In this study, as predicted, bats were shown to spend longer periods roosting from mid-August onwards until after the first week in November (at which point mean ambient temperatures were around 10°C and mean skin temperatures were around 15°C) when they spent prolonged periods in the roost, and torpor. Thus the onset of hibernation appears to occur at the start of November. No bats were active when ambient temperatures dropped below 6°C. This is supported by a study by Webb *et al.* (1996) which found that Vespertilionid bats hibernated with a range of temperatures from -10 to 21°C, with a mode of 6°C.

Our data supported the hypothesis that *N. leisleri* in Ireland do not undertake long-distance migrations and observed dispersal between summer, mating and winter roost sites was, on average, 2 km. The majority of movements occurred between mid-September and late October during the probable mating period (Dietz *et al.* 2009). Shiel *et al.* (1999) carried out a radio-tracking study of *N. leisleri* in the Republic of Ireland and revealed that the mean straight-line distance travelled by juveniles was 19.7 km with distances of two individuals exceeding 34 km. In this study of the pre-hibernal period, similar movements were observed, with the longest straight-line distance of 33.1 km recorded for a single female.

The finding that Leisler's bat in Ireland hibernates within its summer range is in contrast to observations in continental Europe where long migrations have been recorded between summer and winter roost sites, some up to distances of 1,567 km (Ohlendorf *et al.* 2000). Generally, however, this migratory behaviour has been observed in regions where ambient temperature variations are extreme (Likhachev, 1980; Panyutin, 1980; Ohlendorf *et al.* 2000; Dondini *et al.* 2012). We suggest that the temperate oceanic climate in Ireland provides environments favourable in both the summer and winter months for

Vespertilionids explaining the sedentary behaviour.

Bat boxes appeared to be important for Leisler's bats in this study: the majority of tagged bats were initially located in bat boxes which were in use until the end of October. They seemed to augment the few apparent roosting opportunities offered by the mixed, mostly coniferous forest in the present study. Leisler's bats are known to exhibit a mating system characterized by resource defence polygyny (Bogdanowicz and Ruprecht, 2004), with mating groups of one male and up to 10 females (Helvesen & Helvesen, 1994). This seasonal use of bat boxes and the observation of several females to a single male in these bat boxes suggested that these were being used as mating roosts, as seen in other studies (e.g. Dondini and Vergari, 2009).

We found that *N. leisleri* in Ireland are dependent on features in buildings and splits or holes in trees throughout the pre-hibernal period, but that trees were used almost exclusively after November, particularly deciduous trees demonstrating the importance of these roost sites for hibernating *N. leisleri*. Several bats, however, were observed using domiciles until mid-November when the batteries in their transmitter expired.

Despite the habitat surrounding roosts being predominantly coniferous, tree roosts used by *N. leisleri* were located predominantly in oak (*Quercus* spp.) and beech (*Fagus* spp.) trees. Similarly, *N. leisleri* in Poland used oaks and ash (*Fraxinus* spp.) (Ruczynski and Bogdanowicz 2005), while bats in Switzerland selected chestnut trees during the pre-hibernal period (*Castanea sativa*) (Spada *et al.* 2008). Although rot holes, exfoliating bark and crevices were utilised by bats, by far the most common tree roost type was splits in the trunk or tree branch and of these, the majority were located in oaks (Ruczynski and Bogdanowicz 2005). It is not known whether oaks were selected as they are more likely to contain splits or whether there was simply a greater number of oaks in proportion to other deciduous tree types used as roosts within the study sites. The majority of roosts were on, or close to, forest edges and paths, possibly because tree cavities closer to the edge of woodland and trees in less dense woodland may experience increased diurnal temperature through solar exposure (Kurta *et al.* 1993; Vonhoff and Barclay 1996; Brigham *et al.* 1997) or because of increased susceptibility to wind damage. Although Leisler's bats usually forage high above the ground, on emergence from roosts, when light levels are high, they often tend to follow linear landscape elements (Russ *et al.* 2003). It is possible therefore that roosts that are located close to these linear elements will be selected. In addition, wing loading of Leisler's bats is high and thus the species is not very manoeuvrable in cluttered environments (Dietz *et al.* 2009) and thus it is likely that roosts located on the edges of clutter will be selected rather than in the centre. This is supported by a study by Spada *et al.* (2008) of roost selection in Leisler's bat, which found roosts were more often in open forest patches with low tree density.

This study additionally revealed that buildings, domiciles and non-domiciles are important for Leisler's bats in Northern Ireland during the pre-hibernal period. Domiciles are particularly important in Ireland during the maternity period (Allen *et al.* 2000). However, non-domiciles, such as barns, byres and uninhabited houses were also used, particularly from late-August until late-October, while several bats were observed using domiciles until mid-November during the hibernal period.

With the knowledge that populations of *N. leisleri* in Northern Ireland are sedentary, a priority for the conservation of this species should now be the identification and protection of both pre-hibernal and hibernation roost sites, the nature of which was previously unknown. While this study again highlights the importance of buildings for Irish populations of Leisler's bats, it also suggests that deciduous trees with splits and rot holes are an important resource to bats during the hibernal period. The protection of older trees, particularly oak and beech should be a conservation priority.

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References

- Aldridge HDJN, and Brigham R M (1988) Load carrying and maneuverability in an insectivorous bat: a test of the 5% “rule” of radio-telemetry. *Journal of Mammalogy* 69:379–382.
- Allen P, Forsyth I, Hale P and Rogers S (2000) Bats in Northern Ireland. *Special Zoological Supplement 2000. The Irish Naturalist’s Journal*.
- Beer JR and Richards AG (1956). Hibernation of the Big Brown Bat. *Journal of Mammalogy* 37:31-41
- Bogdanowicz W, Ruprecht AL (2004) *Nyctalus leisleri* (Kuhl, 1817) – Kleinabendsegler. In: Krapp F. (Ed.). *Handbuch der Säugetiere Europas. Band 4/II: Fledertiere (Chiroptera) II*. Wiebelsheim, pp 717-756.
- Brigham RM, Vonhof MJ, Barclay RMR and Gwilliam JC (1997) Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). *Journal of Mammalogy* 78:1231-1239.
- Dietz C, Helversen OV and Nill D (2009) Bats of Britain, Europe and northwest Africa. A and C Black, London, UK, pp 400.
- Dondini G and Vergari S (2009) Harem size and male mating tactics in *Nyctalus leisleri* (Kuhl, 1817) (Chiroptera, Vespertilionidae). *Hystrix* 20(2):147–154.
- Dondini G, Rutkowski T, Vergari S and Wojtaszyn G (2012) Long distance migration of female Leisler’s bat (*Nyctalus leisleri*) from Italy to Poland. *Hystrix*, 23(2):93-94.
- Fairley J (2001) A basket of weasels. Privately published, Belfast.
- Fenton MB and Thomas DW (1985) Migrations and dispersal of bats (Chiroptera). *Contributions to Marine Science (Special supplement: Migration: Mechanisms and Adaptive Significance, ed. M. A. Rankin)*, 27:409-424.
- Formozov AN (1966) Adaptive Modifications of Behavior in Mammals of the Eurasian Steppes. *Journal of Mammalogy* 47:208-223
- Helversen OV and Helversen DV (1994) The “advertisement song” of the lesser noctule bat (*Nyctalus leisleri*). *Folia Zool.* 43:331–338.
- Hutterer R, Ivanova T, Meyer-Cords C and Rodrigues L (2005) Bat migrations in Europe: a review of banding data and literature. *Naturschutz und Biologische Vielfalt* 28:1–176.
- Hyndman RJ, Athanasopoulos G, Razbash S, Schmidt D and Zhou Z (2012). forecast: Forecasting functions for time series and linear models. R package version 4.00. <http://CRAN.R-project.org/package=forecast>
- Jia JS, Zhao JZ, Deng HB and Duan J (2010) Ecological footprint simulation and prediction by

ARIMA model-A case study in Henan Province of China. *Ecological Indicators* 10.2: 538-544.

Kunz TH and Lumsden LF (2003) Ecology of cavity and foliage roosting bats. In: *Bat Ecology* (T.H. Kunz and M.B. Fenton eds.), The University of Chicago Press, Chicago.

Kurta A, King D, Teramino JA, Stribley JM and Williams K J (1993) Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist* 129:132-138.

Likhachev GN (1980) Bats of Prioksky-terraced Reserve. In: *Bats* (Kuzyakin, A.P. and K.K. Panyutin, eds.). -Moscow, Nauka: 115-154.

McAney K (2006) A conservation plan for Irish vesper bats. *Irish Wildlife Manual*, 20:1–57.

McManus JJ (1974) Activity and Thermal Preference of the Little Brown Bat, *Myotis lucifugus*, during Hibernation. *Journal of Mammalogy* 55:844-846

McNab B (1982) Evolutionary Alternatives in Physiological Ecology of Bats. In T. Kruz, ed. *Ecology of Bats*. New York, Plenum Press, pp. 151-196

Neuweiler G (2000) *The Biology of Bats*. Oxford University Press.

Ohlendorf B, Hecht B, Strassburg D and Agirre-Mendi P (2000) Fernfund eines Kleinabendseglers (*Nyctalus leisleri*) in Spanien. *Nyctalus*, 7: 239-242

O'Sullivan P (1994) Bats in Ireland. *Irish Naturalist's Journal*. Special Zoological Supplement.

Panyutin K. (1980) Bats. Pp. 23-46. In: (Kucheruk V.V.; ed.): *Results of marking animals*. Nauka, Moscow, 296pp.

Pop JW (1989) Food-storage in artificial nest-boxes by the white-footed mouse, *Peromyscus leucopus*. *Canadian field-naturalist* 103:410-411.

R Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

Ruczynski I and Bogdanowicz W (2005) Roost cavity selection by *Nyctalus noctula* and *N. leisleri* (Vespertilionidae, Chiroptera) in Białowieża primeval forest, Eastern Poland. *Journal of Mammalogy*, 86:921–930.

Russ JM, Briffa M, Montgomery WI (2003) Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *Journal of Zoology* 259:289-299.

Ryan BF, Joiner BL (1994) *Minitab Handbook* 3rd edition. Duxbury Press.

Schober W, Grimmberger E (1997) Bats of Britain and Europe. London. Hamlyn Publishing Group.

Shiel CB, Duverge PL, Smiddy P, Fairley JS (1998) Analysis of the diet of Leisler's bat (*Nyctalus leisleri*) in Ireland with some comparative analyses from England and Germany. *Journal of Zoology (London)* 246:417-425.

Shiel CB, Fairley JS (1998) Activity of Leisler's bat *Nyctalus leisleri* (Kuhl) in the field in south-east County Wexford, as revealed by a bat detector. *Biology and Environment: Proceedings of the Royal Irish Academy* 98B:105-112.

Shiel CB, Shiel RE, Fairley JS (1999) Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *Journal of Zoology (London)* 249:347-358.

Spada M, Szentkuti S, Zambelli N, Mattei-Roesli M, Moretti M, Bontandina F, Arlettaz R, Tosi G, Martinoli A (2008) Roost selection by non-breeding Leisler's bats (*Nyctalus leisleri*) in montane woodlands: implications for habitat management. *Acta Chiropterologica*, 10:81-88.

Stebbing R E, Griffith F (1986). *Distribution and Status of Bats in Europe*. NERC, Monks Wood, UK.

Strelkov PP (1969) Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. *Acta Zoologica Cracoviensia*, 14:393-440.

Vonhof MJ, Barclay RMR (1996) Roost site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology*. 74:1797-1805.

Waters D, Jones G, Furlong M (1999) Foraging ecology of Leisler's bat (*Nyctalus leisleri*) at two sites in southern Britain. *Journal of Zoology, London*, 249:173-180.

Webb P I, Speakman JR, Racey PA (1996) How hot is a hibernaculum? A review of the temperature at which bats hibernate. *Canadian Journal of Zoology*. 74:761-765

Willis CKR, Brigham RM (2003) Defining torpor in free-ranging bats: Experimental evaluation of external temperature sensitive radio-transmitters and the concept of active temperature. *Journal of Comparative Physiology B*. 173:379-389.

Appendix 1. Details of tagged Leisler's bats

ID	Date	Location	Roost type	Sex	Forearm length (mm)	Weight (g)	Tag (HoloHil Systems Ltd.)	Tag weight (g)	Duration (nights)
75590	29-jul-02	Belfast	Building	F	44	14.0	LB-2	0.56	No data
75536	31-jul-02	Belfast	Building	F	45	16.0	LB-2	0.56	No data
75589	31-jul-02	Belfast	Building	F	43	14.0	LB-2	0.56	No data
75588	1-ago-02	Belfast	Building	M	43	14.0	LB-2T	0.58	6
75587	12-aug-02	Belfast	Building	F	44	17.0	LB-2T	0.58	12
75537	22-aug-02	Belfast	Building	M	44	17.5	LB-2T	0.58	21
72291	29-aug-02	Belfast	Building	F	43	17.0	LB-2T	0.58	11
75538	11-sep-02	Tollymore	Bat box	F	43	18.0	LB-2T	0.58	26
75540	16-sep-02	Tollymore	Bat box	F	45	22.0	LB-2T	0.58	36
75540	16-sep-02	Tollymore	Bat box	M	42.4	18.0	LB-2T	0.58	31
75581	24-sep-02	Tollymore	Bat box	F	43	17.0	LB-2T	0.58	24
75607	24-sep-02	Tollymore	Bat box	M	42	18.0	BD-2AT	0.78	30
75608	10-oct-02	Tollymore	Bat box	F	44	21.5	BD-2AT	0.78	32
75611	10-oct-02	Tollymore	Bat box	F	42	19.0	BD-2AT	0.78	31
75612	10-oct-02	Tollymore	Bat box	F	45	21.0	BD-2AT	0.78	29
75601	10-oct-02	Tollymore	Bat box	F	43	20.0	BD-2AT	0.78	No data
75602	10-oct-02	Tollymore	Bat box	M	44	17.5	BD-2AT	0.78	31
75541	23-aug-03	Belfast	Building	F	46	18.5	LB-2T	0.90	No data
75582	23-aug-03	Belfast	Building	F	43	18.0	LB-2T	0.90	20
75583	19-sep-03	Belfast	Building	F	45	20.0	LB-2T	0.90	28
75584	19-sep-03	Belfast	Building	M	43	18.5	LB-2T	0.90	30
75610	2-oct-03	Tollymore	Bat box	F	42	20.5	LB-2T	0.90	12
75592	2-oct-03	Tollymore	Bat box	M	44	18.5	BD-2A	0.90	25
85999	6-oct-03	Tollymore	Bat box	F	43	19.2	BD-2A	0.90	86
86000	6-oct-03	Tollymore		F	N/A	19.5	BD-2T	0.92	54
75609	6-oct-03	Tollymore		F	N/A	18.0	BD-2T	0.92	27
85996	7-oct-03	Tollymore		F	N/A	18.5	BD-2T	0.92	77
85997	7-oct-03	Tollymore		F	N/A	20.5	BD-2T	0.92	68
85998	7-oct-03	Tollymore		F	44	22.0	BD-2T	0.92	67