ORIGINAL ARTICLE

Interspecific cohabitation of maternity colonies of *Nyctalus noctula* and *Myotis daubentonii* (Chiroptera: Vespertilionidae) in a single roost feature in the West Midlands, UK

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ABSTRACT

Woodland bat species may 'time share' tree roost features and occasionally have been recorded cohabiting in low numbers. However, few observations exist of substantial maternity roosts of sympatric species cohabiting in a single roost feature. Following an emergence survey in June of 2021 of a known maternity roost of 28 *Nyctalus noctula* individuals (pre-parturition), a further emergence from the same feature of 59 *Myotis daubentonii* was recorded and filmed using infra-red and thermal cameras. Cohabitation records of maternity colonies of this size have not been previously submitted to the UK Bat Tree Habitat Key database, nor do similar observations appear in the literature. Following the 2021 destruction of the roost feature during a storm, we were able to describe the entire feature in detail, including transverse section analysis and photography. Subsequent surveys have now shown that these two bat species have cohabited in features in at least three separate trees within the study site (a small, suburban, broad-leaved woodland), over at least two seasons. This novel record of interspecific cohabitation not only adds to the body of knowledge regarding roost cohabitation of Vespertilionidae in temperate woodlands, but also highlights the value of infra-red and thermal optics for improving the efficacy of bat emergence surveys, particularly in forest habitats.

INTRODUCTION

Little is known about the sharing of roost features by bats, particularly by Vespertilionidae (Zeus et al. 2017, Salinas-Ramos et al. 2020). Sharing of roost features can be broadly categorised as either conspecific (separate colonies of the same species) or interspecific (colonies of different species), and as either 'time-sharing' (utilization of the same roosting feature at different times) as coined by BTHK (2018) or cohabitation (simultaneous use of the feature by more than one colony).

Salinas-Ramos et al. (2020) found no evidence that roost feature availability was a factor in interspecific competition, but acknowledged the rarity of analysis of roost features as a resource for which bats compete. External factors may play a role, such as the presence of invasive species as competitors for roosts (Welch & Leppanen 2017). Whilst cohabitation between bat species such as brown long-eared bat (*Plecotus auritus*) and grey squirrel (*Sciurus carolinensis*) has been documented and even photographed (BTHK 2018), other species may represent more direct competition. In

the case of this study, the ring-necked parakeet (*Psittacula krameri*) has recently established a population in the study site. The presence of this species has been documented to correspond to a decrease in *N. noctula* populations through roost competition (Giuntini et al. 2022), and as such the presence of this species may place pressure on *N. noctula* or other bats which utilise similar features.

In a study of the use of bat boxes by *Myotis bechsteinii, Myotis nattereri* and *P. auritus*, Zeus et al. (2017) recorded frequent time-sharing by *P. auritus* and *M. nattereri*, but no instances of interspecific cohabitation in any boxes, though *P. auritus* did avoid roost features that had been previously utilised by their conspecific groups. In another study of interspecific use of bat boxes spanning five years, researchers recorded 27 roosts being time-shared by both *M. nattereri* and *Myotis daubentonii*, but never at the same time (August et al. 2014).

Historical records exist for interspecific cohabitation of small numbers of bats. The earliest published record appears to be from Barrett-Hamilton (1910) who referred to *Rhinolophus hipposideros* and *Rhinolophus ferrumequinum*

being encountered together where they are sympatric, and stated that "most other small bats do not object to the presence of an alien" Barrett-Hamilton (1910 p27), but noted that *Nyctalus noctula, Nyctalus leisleri* and *Eptesicus serotinus* were not known to cohabit with other species. Nyholm (1965) reported from Finland a mixed colony of *Myotis mystacinus* and *Eptesicus nilssonii* in Kustavi in 1951 (numbers of individuals not recorded), the same two species in Konnekoski in 1953 (four individual *E. nilssonii* within a larger colony of *M. mystacinus*) and again in Kastelholm in 1956; followed by a record of a *M. daubentonii* nursery roost containing two *M. mystacinus* females in Rautelankoski in 1958. Nyholm (1965) also made reference to Ryberg (1947), who reported *M. daubentonii* and *M. mystacinus* roost-sharing with *Pipistrellus pipistrellus*, *P. auritus* sharing a roost feature with *M. daubentonii* and one record of a *M. daubentonii* maternity colony in which was found a single male *N. noctula*. This latter record appears to be the only published incidence of cohabitation of these two species.

In a recent meta-analysis, cohabitation has been recorded in *Rhinolophidae* in at least 15 open roosting spaces (e.g., attics, caves), with roosts comprising *R. hipposideros* with small numbers of *R. ferrumequinum* (both of which are void-dwelling species). No cohabitation of members of *Vespertilionidae* (largely crevice-dwelling species) was recorded (Salinas-Ramos et al. 2020). These authors acknowledged that the tendency of tree cavities to be narrower features may be a factor in their observation that multi-species roosting is uncommon in forest-dwelling bats. The United Kingdom roost database held by the Bat Tree Habitat Key (http://battreehabitatkey.co.uk) held (at the time of access) 1,789 confirmed roost records representing 820 roost features. Of those, 498 records representing 108 roost features were of time-sharing (being records of species in roost features that have been recorded to support other species), indicating that 13.17% of features were used by more than one species. Records of cohabitation are far fewer, comprising eight records representing six unique roost features, indicating that 0.73% of features are recorded as interspecific cohabitation roosts. Of the six features, the highest number of bats cohabiting at any one time is four, and the number of cohabitation roosts recorded during the pregnancy or nursery season (June – August) is three. A 2003 report of the findings of a survey in June 2002 at Briddlesford Copse, Isle of Wight, UK (Davidson-Watts 2003) detailed an observation of 12 *N. noctula* emerging from a woodpecker hole in a *Fraxinus excelsior* followed by 57 *Myotis bechsteinii*.

In this manuscript we discuss an important new record of interspecific cohabitation of maternity colonies of *Myotis daubentonii* and *N. noctula* in a deciduous woodland in the West Midlands, United Kingdom. This is the first published record of interspecific cohabitation of colonies of this size in a tree roost for Great Britain.

MATERIALS AND METHODS

Roost identification and location

On 24/07/2020, a substantial pile of bat droppings was reported to the authors, having been found below a potential roost feature in a mature oak (*Quercus robur*) in Merrions Wood Local Nature Reserve. The reserve comprised 8.18 ha of broadleaved woodland (predominantly *Q. robur* and planted beech (*Fagus sylvatica*) in a broadly suburban context, lying approximately 8 km NE of the city of Birmingham in the West Midlands, UK (52°33'39.9"N 1°56'18.9"W).

Roost characterisation survey (2020)

The roost feature (hereafter 'RF1') was subject to a roost characterisation survey (Collins 2016) on the same day to determine the demographic composition and nature of the colony. A sample of the bats occupying the roost was captured (in this case, utilising a 6 m, double-high monofilament 'Ecotone M' mist net placed approximately 3 m away from the roost aperture) under Natural England (NE) project licence [2019-44132-SCI-SCI]. The survey utilised standard Advanced Bat Licence Survey Technique (ABLST) methods (Kunz & Kurta 1988, Barlow 1999, Collins 2016). Once the sample was collected, the net was removed, and the remainder of the colony (of hitherto undetermined size and species composition) was allowed to emerge unhindered.

Emergence surveys (2020)

On 26/07/2020 it was determined that the roost was no longer present in RF1. By utilising a heterodyne bat detector and walking the woodland paths prior to emergence, we determined that the colony had moved to a second roost feature (hereafter 'RF2'): a pair of 12 m high woodpecker holes on the southern aspect of a second mature *Q. robur*, approximately 210 m east of RF1. An emergence survey of the bats within that feature was conducted that evening, aided by hand-held, non-recording infra-red optics (Newton NV3 14062). Survey timings and environmental conditions for this and all subsequent emergence surveys were in keeping with current UK survey guidelines (Collins 2016), with the survey commencing 15 minutes prior to sunset (21:16) and continuing until two hours after sunset (23:31) BST (Bikos et al. 2021).

Aerial inspection (2020)

All aerial inspections were undertaken by qualified tree climbers [City and Guilds City & Guilds Tree Climbing and Aerial Rescue CS38] operating under NE bat survey class licences [2019-40450-CLS-CLS and 2019-40449-CLS-CLS] using Ridgid Seesnake endoscopes. On-ground data to support endoscope inspections were collected utilising standard Bat Tree Habitat Key methods (Andrews 2020) comprising measurements of the tree and feature (where access and equipment allowed) as well as a description of the internal characteristics of the void. Aerial inspection of RF1 took place on 17/07/2020 to determine the feature's internal characteristics.

Emergence surveys (2021)

Visual observations for all 2021/2022 emergence surveys were supported using one infra-red camera (Panasonic HC-VX980 or Canon XA20) and infra-red flood light arrays, a Nightfox XB5 infrared spotlight and a Track

IR35 Pro thermal scope. Infra-red footage was analysed using Lightworks software (WKS Software Ltd 2021); thermal footage was analysed using TrackIR for Android (Wuhan Guide Infra-red Co 2019). Acoustic recordings of emerging bats were also collected using a Batlogger M full-spectrum bat detector, manually analysed using Elekon Bat Explorer Pro (Elekon sAG, 2019) utilising standard texts (Russ 2012, 2021, Middleton et al. 2014). Acoustic recordings were utilised for determination of species only, in coordination with review of footage; bat passes were not defined due to the abundance of post-emergence foraging bats precluding meaningful analysis. After a daytime visit on 12/06/2021 had determined the colony to have returned to RF1, an emergence survey was undertaken that evening; this was followed by surveys of RF1 on 14/06/2021 and 09/07/2021 to gather additional footage and recordings. Production of density plot of emergence timings was undertaken using the ggplot2 package (Wickham 2016) in R studio (R Development Core Team 2014).

Dissection and aerial inspection of RF1 (2021)

On 29/07/2021, the limb bearing RF1 was brought down when Storm Evert struck the UK. On 05/08/2021, we supervised the removal of the fallen limb from the public footpath, at which time the limb was inspected for the presence of bats and was cut into five sections, under bat survey class licences [2017-32644-CLS-CLS and 2015-17357-CLS-CLS], with each section being cut lengthways to allow the inspection and measurement of the internal void. The sections were numbered proximally to distally, with section 1 being that remaining in-situ. Measurements of external diameter, length, and internal diameter of each section were recorded. Roosting locations for both bat colonies were identified by the presence of staining and droppings (with the distal extent of those staining areas used for the purposes of measurement). An aerial inspection of section 1 of RF1 took place on 28/08/2021 to determine the internal dimensions of that section of the feature.

Emergence surveys (2022)

An emergence survey was undertaken of RF2 on 23/07/2022 following the protocols detailed above. On 26/07/2022 the colony was determined to have left RF2. A series of roost-finding surveys (comprising walking the woodland prior to sunset using bat detectors and listening for *N. noctula* social calls) and subsequent emergence surveys were undertaken throughout the woodland. These followed the movements and roost-switching patterns of the *N. noctula* maternity colony. During this time, an additional *N. noctula* roost was found, and was determined (by emergence surveys and hand netting) to be a roost of 7 mature male bats. Where emergence counts consistently indicated large numbers of bats, these were inferred to be the main maternity roost. These surveys comprised those of a south-facing knot hole in a mature *Q. robur* on 31/07/2022 (hereafter RF3) and an extensive callus roll around a lightning strike on a fourth *Q. robur* on 03/08/2022 (hereafter RF4). On 12/08/2022, the colony of *N. noctula* was located in a wound in a mature *F. sylvatica* (hereafter RF5), and was noted to be sharing that feature with *M. daubentonii*.

Roost trapping (2022)

The shared roost RF5 was subject to emergence trapping under licence on 19/08/2022, with the aim of capturing and applying rings to the *N. noctula*, to facilitate future monitoring and data-gathering on individual movements and roost fidelity. As an alternative to the use of static hand nets, to minimize disturbance and maximise catch efficacy, a Faunatech™ Austbat mini 1m² mini mine-shaft trap was positioned in front of the aperture for the duration of emergence.

Aerial inspections of RF2, and RF5 (2023)

On 07/01/2023, aerial inspections of the internal characteristics of RF2 and RF5 were undertaken by qualified and licensed tree climbing bat ecologists. Characteristics were recorded according to the Bat Tree Habitat Key database.

RESULTS

Roost characterisation (2020)

The sample comprised 11 individual *N. noctula*, comprising seven parous females, three juvenile males and one juvenile female, a demographic composition indicative of a maternity roost.

Emergence survey (2020)

The survey on 26/06/2020 yielded a total emergence count of 70 individual bats from RF2. The species composition of this colony was assumed at the time to be that of *N. noctula* only due to lack of evidence to the contrary (i.e., interspecific cohabitation had not yet been recorded).

Emergence surveys (2021)

The emergence survey of RF1 on 12/06/2021 recorded 28 individual *N. noctula* emerging from the proximal aperture (between sunset +00:22 and sunset +00:33) (Fig. 1A), with at least one individual remaining in the roost. This was followed by the subsequent emergence of 59 *M. daubentonii* from the same aperture (between sunset +00:39 and sunset +00:67) (Fig. 1B), with an interval of six minutes between the last emergence of *N. noctula* and the first emergence of *M. daubentonii* (Fig. 2). No bats were observed exiting the second (upper) aperture. Infra-red footage of the emergence is available at [https://youtu.be/bRBIjeD1SQA].

Aerial Inspection (2020)

RF1 was located in the lowest secondary branch of a living, mature *Q. robur* approximately 25 m in height and 80 cm in diameter at breast height (DBH). The union of the stem with the primary branch was at a height of 3.5 m, where the primary branch had a diameter of 53 cm. The feature (Fig. 3) presented two apertures: the first (proximal) aperture was an 8 cm diameter knot hole, on the northeast aspect of the secondary branch and lying 87 cm from the primary branch of the tree at an angle of approximately -15 degrees (i.e., slightly downward pointing) and 6 m above ground
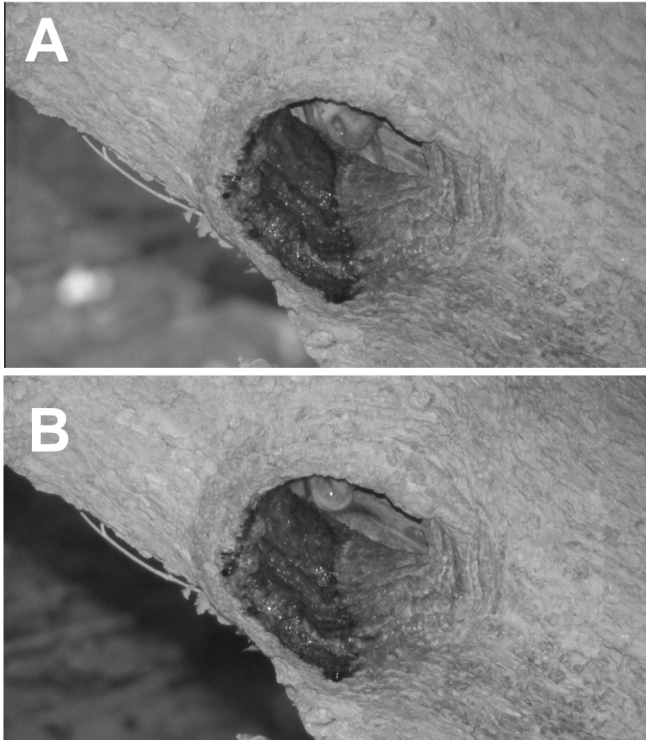
Fig. 1 - A) *Nyctalus noctula* prior to emergence from proximal aperture of RF1; B) *Myotis daubentonii* prior to emergence from proximal aperture of RF1.
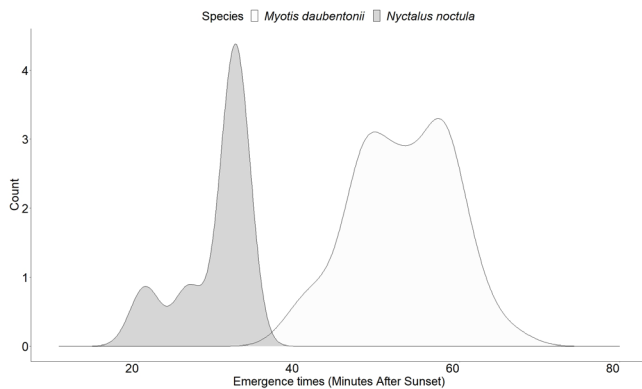

Fig. 2 - Density plot of emergence of *Nyctalus noctula* and *Myotis daubentonii* from RF1 roost on 12/06/2021.

level. The diameter of the branch at the location of the proximal aperture was 32 cm. The second (distal) aperture was a knot hole with an external diameter of 8 cm closing to an internal diameter of 3 cm and was situated 440 cm out from the proximal aperture. It also lay on the northeast aspect of the branch, with a horizontal (90 degree) angle, lying approximately 4 m above ground level (this figure is an estimate based on measurements from the fallen limb) and with a diameter of 23 cm at the point of the aperture.

Dissection and aerial inspection of RF1 (2021)

The total internal length of the roost feature from base to top was 615 cm. The distance from the proximal aperture to the apex was 555 cm, and distance from the proximal aperture to the base was 50 cm. The distance from the distal aperture to the apex was 115 cm and the distance from the secondary aperture to the base was 527 cm. Measurements of each section of the feature are presented in Fig. 4, with the branch supporting the roost feature having an average diameter of 32 cm at section 1 (the section supporting the proximal aperture), reducing to 23 cm in section 5 (the section supporting the distal aperture) and then to 20 cm at section 6.

The staining from the *N. noctula* roosting location (Fig. 5A) began (i.e., at its distal point) in section 3 of the limb approximately 180 cm above the proximal aperture in section 1; the staining from the *M. daubentonii* roosting location (Fig. 5B) began in section six of the limb approximately 90 cm above the distal aperture in section 5, and a total of 530 cm above the proximal aperture. Internal characteristics following Bat Tree Habitat Key recording methodology (Andrews 2020) were classified having smooth substrate, dry humidity and a spire-shaped apex (based on the assessments on 17th July 2021 and 5th August 2021).

Emergence Surveys (2022)

Only one *N. noctula* maternity roost was found during any night, and no evidence exists to suggest multiple roosts of the species being present within the woodland. The emergence survey on 23/07/2021 of RF2 yielded a total of 88 bats comprising 39 *N. noctula* (emerging from sunset +00:10
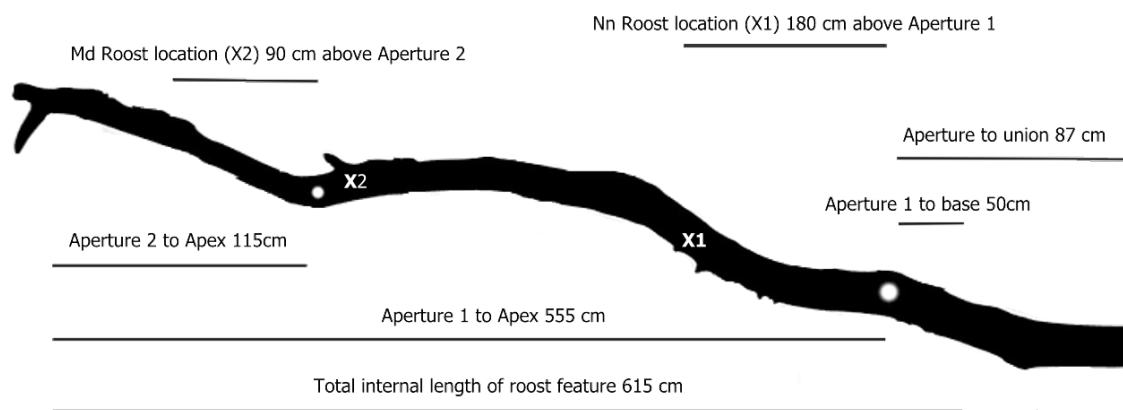

Fig. 3 - Schematic of internal roost measurements of RF1. Roosting locations of colonies (as indicated by location of droppings/staining denoted by 'Md' (*Myotis daubentonii*) and 'Nn' (*Nyctalus noctula*).

Fig. 5 - A) *Myotis daubentonii* staining/roosting location; B) *Nyctalus noctula* staining/roosting location.
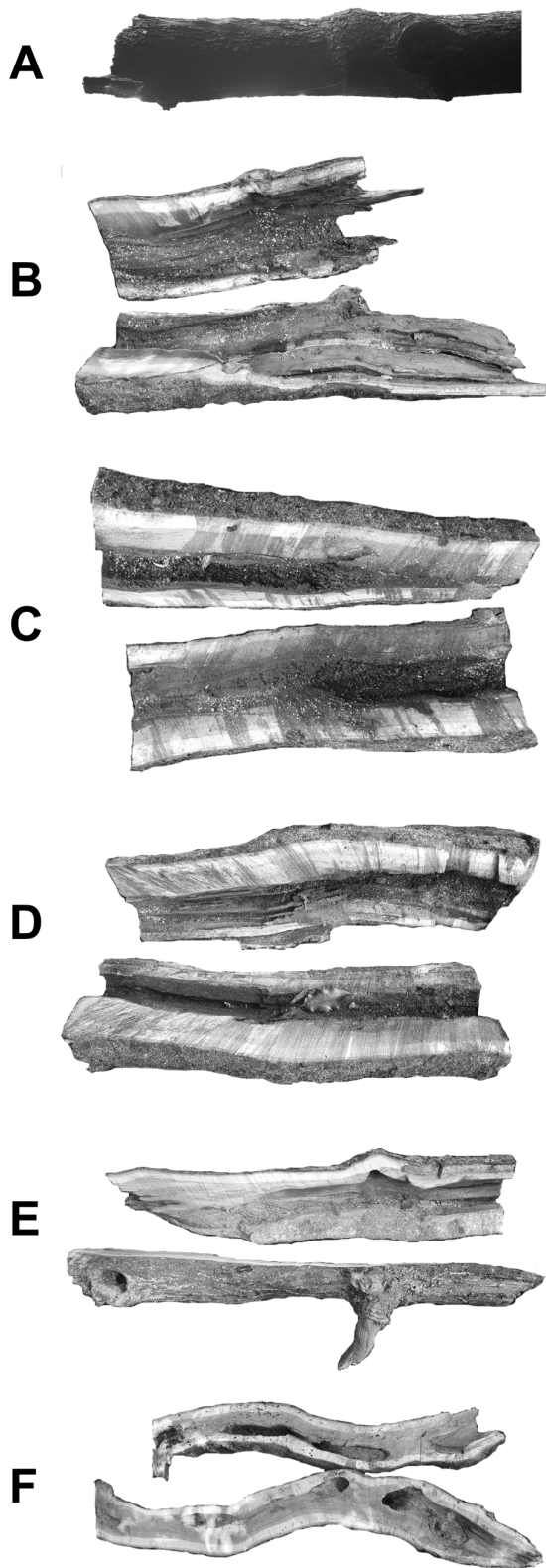
Fig. 4 - Transverse sections of roost feature RF1. A) Section 1 (in-situ); L=147 cm; D=32 cm; DV=25 cm; B) Section 2; L=101 cm; D=26 cm; DV=16 cm; C) Section 3; L=69 cm; D=24 cm; DV=12 cm; D) Section 4; L=75 cm; D=23 cm; DV=10 cm; E) Section 5; L=118 cm; D=23 cm; DV=10 cm; F) Section 6; L=105 cm; D=20 cm; DV=10 cm. Abbreviations: L, length; D, mean diameter of section; DV, diameter of void.
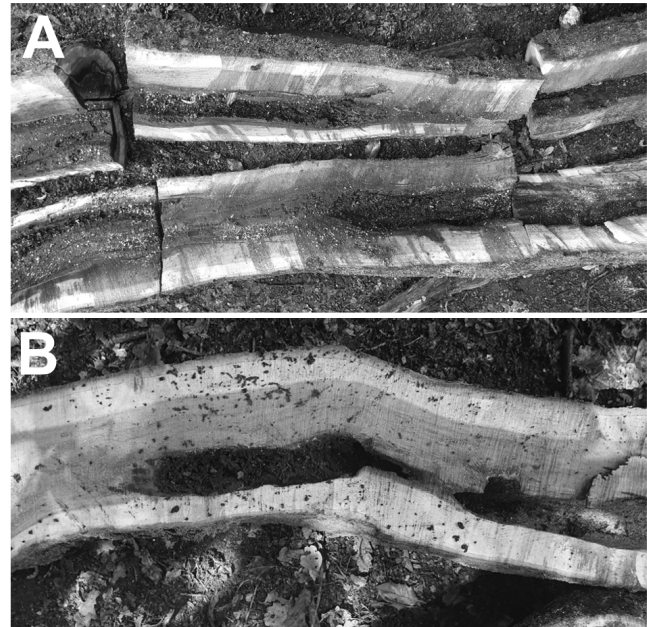
to sunset +00:29) and 49 *M. daubentonii* (emerging from sunset +00:31 to sunset +00:52). The *N. noctula* maternity roost had switched to R3 on 31/07/2022 comprising 41 individual bats, with no *M. daubentonii* recorded. The emergence survey of R4 on 03/08/2022 yielded a count (with only partial visibility of the roost feature) of at least 18 *N. noctula* (though acoustic recordings indicated emergence of many more), with numerous calls of *Myotis* bats recorded, but no accompanying visual observations. The emergence survey of RF5 on 12/08/2022 yielded a count of two *N. noctula* and 29 *M. daubentonii* (most *N. noctula* had left the roost well before sunset and their emergence was missed). Both species appeared to utilise separate internal chambers above the aperture, but later-emerging *N. noctula* and earlier-emerging *M. daubentonii* utilised the aperture at the same time, with no observed interactions between species (Fig. 6).

Roost trapping (2022)

The roost trapping survey of RF5 undertaken on 19/08/2022 resulted in the successful capture of 22 individual *N. noctula* comprising females and juveniles of both sexes (all of which were ringed under licence on the night of survey). Several bats were observed evading the trap on emergence and this number is considered an underestimation of the colony size. In addition, over 40 *M. daubentonii* were captured (all of which were released at the roost without being ringed due to licensing restrictions).

Aerial inspections of RF2 and RF5 (2023)

The aerial inspections of RF2 and RF5 on 07/01/2023 provided further data on the internal characteristics of both of these cohabitation roosts. At the time of survey, RF2 was unoccupied by bats, affording access to the entirety of the feature. The access point to the void was a pair of woodpecker holes at the union of the primary branch and

Fig. 6 - Individual *Nyctalus noctula* and *Myotis daubentonii* in the aperture of RF5. Infra-red footage shows *N. noctula* utilising a rear chamber and *M. daubentonii* utilising a front chamber.

stem of a mature *Q. robur* approximately 30 m in height with a DBH of 80 cm. The apertures (one above the other and separated by 10 cm) were internally connected by a link of approximately 25 cm. Both had a southern aspect, at a height of approximately 12 m, where the diameter of the branch was 27 cm. Internally, the lower aperture (8 cm x 5 cm) led to an inner chamber with a depth of 24 cm, width of 24 cm and height of 38 cm, where its apex was dome shaped. This feature also extended downwards. The upper (forward) aperture (6 cm x 5 cm) led to a chamber with a depth of 10 cm, width of 5 cm and height of 6 cm with a tube-shaped apex. The internal substrate of the void was smooth and dusty, and the internal humidity at the time of survey was dry. At the time of inspection, RF5 was occupied by two *N. noctula* (one was a ringed male) which were present in the rear chamber of the feature. The access point to the void was a wound with a south-west aspect 4.5 m in height in the stem of a mature *F. sylvatica* with a DBH of 94 cm. The aperture height was 15 cm x 7 cm and led to a complex, chambered void. The internal measurements were 30 cm wide, 10 cm deep, and the forward chamber was 100 cm high with a domed apex (the rear chamber was not measured due to the presence of bats). The internal substrate was rough and polished, and internal humidity at the time of survey was dry.

DISCUSSION

The results of the last few years of monitoring of these colonies have demonstrated interspecific cohabitation of maternity colonies of *N. noctula* (maximum post-parturition count 41 individuals) and *M. daubentonii* (maximum post parturition count 59 individuals) in at least three roosts, of two tree species, in at least two concurrent seasons.

Interspecific cohabitation roosts such as those described here may be more common than records suggest, and this may be particularly true of maternity roosts due to increased calorific demands (lactation, weight-bearing and increased foraging trips) during the maternity season (Racey & Entwistle 2000). The bats themselves may have limited choice in being able to find a roost of suitable size, or with surrounding habitat that meets the needs of lactating females. In a recent meta-analysis, Laforge et al. (2021) found that bats in landscapes of high heterogeneity (such as this study site) may take advantage of the range of diverse resources nearby and thus utilise a smaller home range size than those in a homogenous landscape. The energetic cost of a lactating female traveling to a nearby feeding patch is greater than that of a non-breeding bat making the same journey. This has been demonstrated to be the case with *Myotis lucifugus* and *M. daubentonii*, if not all vesper bats (Henry et al. 2002, Encarnação et al. 2010). Lactating females must also return to their roost more often to feed their young. To compensate, during this period, females will experience increased predation risk by leaving the roost earlier and increase foraging time (Lučan 2009). Providing cohabiting species are not in direct competition (for either prey or the available space within a roost), this sharing may meet the needs of both colonies.
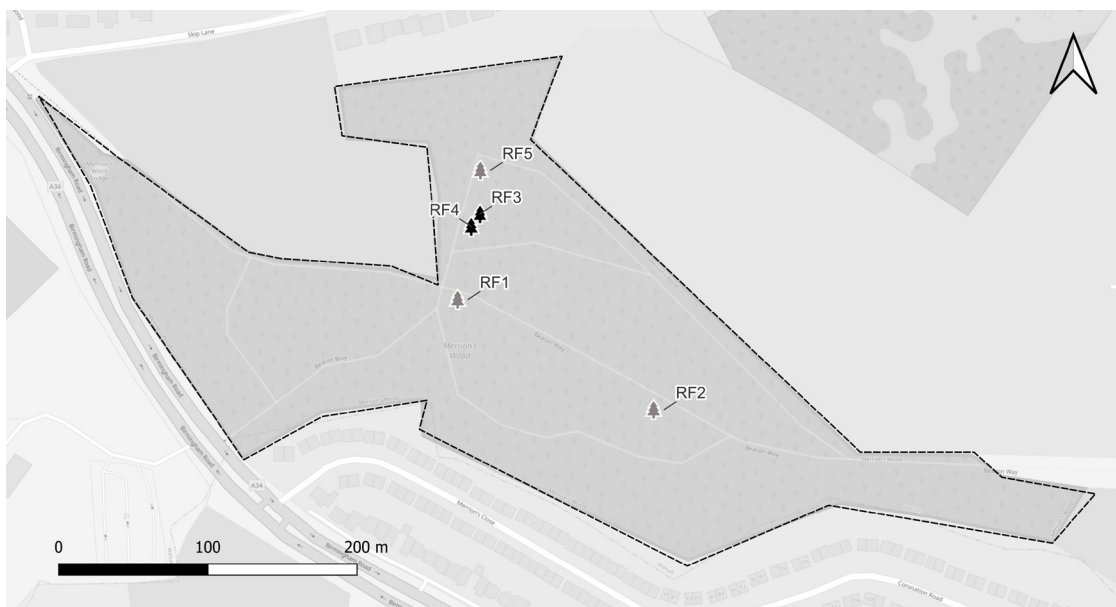

Fig. 7 - Locations of Roosts within Merrions Wood. Interspecific roosts (RF1, RF2 and RF5) shown in grey; *Nyctalus noctula* maternity roosts RF3 and RF4 (without cohabitation observed) shown in black.

In situations where there is competition for large enough roosting features with suitable environmental variables, sharing with another species may represent an efficient solution to the roost resource problem. It has been documented that roost choices (excepting woodpecker holes) for *N. noctula* and *M. daubentonii* are similar (Boonman 2000), whilst their prey are dissimilar, being predominantly Coleoptera and Diptera for *N. noctula* and *M. daubentonii*, respectively (Dietz & Kiefer 2016). In cases where numbers of suitable features large enough to support substantial maternity colonies of each species are limited, this can be addressed by resource partitioning. There are many ways in which bats employ resource partitioning from their sympatric competitors. These include physiological and behavioural adaptations such as staggered emergence and foraging times (Altringham 2003), variability and seasonal plasticity with regard to target prey species (Goiti et al. 2003), partitioning of micro-habitat variables in their feeding grounds (Ciechanowski 2002), and intra-specific, sex-based partitioning of quality feeding grounds during maternity season (Lintott et al. 2014). In our study, the colonies of *N. noctula* and *M. daubentonii* were able to partition their shared roost RF1 as a resource both spatially and temporally. Each of the roost features used for interspecific cohabitation in this study may have been suitable due to their size and/or complexity, as all three roosts afford their inhabitants the opportunity for spatial resource partitioning (different chambers as in RF2 and RF5 or sufficient distances as in RF1). The colonies may also resource partition temporally, as their mean emergence and return times reduce the likelihood of members of either colony encountering the other. In his review of empirical data on the emergence and return of UK bat species, Andrews et al. (2017) reports a mean emergence time for *N. noctula* as 11 minutes after sunset, and a mean emergence time for *M. daubentonii* of 58.1 minutes after sunset. *M. daubentonii* are the first to return, with a mean return time of 40.5 minutes before sunrise, with *N. noctula* returning to roost up to 3 minutes before sunrise. The behavioural idiosyncrasies of these two species mean that in this study, with *M. daubentonii* roosting far above the *N. noctula* colony, the lower roost has emerged by the time the *M. daubentonii* begin to leave the roost, and the route up to their higher roosting position within the feature is still clear upon their return prior to dawn, allowing both colonies to exploit the feature without conflict. Notwithstanding, it is not understood why the smaller, distal aperture of RF1 was not utilised by *M. daubentonii* for emergence, and it is unclear at the point of writing what circumstances led to the early emergence of *N. noctula* from RF5, leading to both species using the aperture simultaneously, foregoing temporal resource partitioning.

Different bat species are known to readily occupy the same roost features at different times of the year for different purposes (BTHK 2018), and while some conspecific colonies avoid even time-sharing, the same colonies have been recorded readily doing so with other species (Zeus et al. 2017). One advantage to utilising the roost features of a different species as opposed to conspecifics may be in a reduced susceptibility to infestations by ectoparasites. Due to the high degree of host specificity in bat ectoparasites (Haelewaters et al. 2018), the roosting spaces of heterospecifics may represent less of a risk. Bats utilise roost switching / fission-fusion behaviour between their favoured roosts to which they exhibit strong philopatry, particularly in females (August et al. 2014). Mobility between such roosts is common (Zeus et al. 2017), particularly in females, fission-fusion behaviour in some Myotis species being particularly well-documented (Kerth & Konig 1999, Kerth et al. 2006, Fleischmann & Kerth 2014). *Nyctalus noctula* potentially roost-switch every 10 days (BTHK 2018) and have been recorded to increase roost-switching frequency during the reproductive period, starting when pups are flightless (Ruczyński & Bartoń 2020).

The data in this study have demonstrated that the Merrions Wood *N. noctula* maternity colony (peak count of 41 individuals) readily switch between at least five roosts within the woodland itself, and three of those roosts have been documented to support their interspecific cohabitation with a substantial maternity colony (peak count 59 individuals) of *M. daubentonii*. Moreover, these colonies (though it is an assumption that the colonies are the same each year, it is not an unreasonable one as natal philopatry has been well-documented (Kerth 2008)) have cohabited for at least two sequential years in three separate roost features. Indeed, it is possible that, given the 2020 emergence count of 70+ bats from RF2 (which exceeds the peak count of either colony alone), that the colonies have been cohabiting for at least three years and moving between these roost features.

Interspecific cohabiting colonies of the size and nature described here are seldom recorded, but it is possible that the phenomenon itself is common, and that the limitations of standard survey methods are partially responsible for under-recording of second or late-emerging bats/colonies from features, particularly in trees/woodlands. The efficacy of emergence surveys once the roost feature can no longer be seen has been demonstrated to reduce, with surveys after that point being likened to 'fixed point activity' surveys rather than emergence surveys (Davidson-watts 2021). In open habitats and under good weather conditions, there is still sufficient illumination (approximately 10.75 lux) at the onset of civil twilight for the human eye to distinguish objects (typically 30–60 minutes after sunset), although under woodland canopy lux levels are far below this (BTHK 2018). The majority of surveys undertaken for bat roosts are carried out following best practice guidelines (Collins 2016). Whilst these guidelines in the UK have helped to standardise survey efforts and recommended the use of night vision aids in certain situations, these methods have been, to date, considered complementary. Interim guidance has recently been issued (Bat ConservationTrust 2022) but are yet to become standard practice commercially. As a result, at least the last half-hour of surveys carried out under existing guidance for emergence surveys (being 15 minutes before sunset to 1.5–2 hours after sunset) are completed in total darkness in which the human eye cannot readily distinguish objects, leaving surveyors with only auditory cues from bat detectors from which to infer bat presence, and from which roost occupancy cannot be reliably determined, as noted by Froidevaux et al. (2020). Given the emergence times of most European bat species (Andrews et al. 2017), it is considered likely that without the use of infrared/thermal imaging, later emerging species may be missed entirely, particularly in wooded habitats. Notwithstanding the difficulting in

locating bat roosts in the first place, this under-recording may be exacerbated due to the poor likelihood of, even with a known roost, the bats being present on the day of survey (Andrews & Gardner 2015).

CONCLUSION

Our study provides a direct observation of two sympatric bat species cohabiting within three separate trees roosts in two tree species over at least two active bat seasons; a hitherto poorly recorded behaviour in *Vespertilionidae*, and the only reported observation of interspecific cohabitation of colonies of this size in the United Kingdom. Furthermore, unique circumstances allowed the feature to be dissected and inspected following recent use by its occupants, thus representing a unique opportunity to present details regarding one roost feature that may assist in the identification of similar features in the future. We believe that due to the intrinsic poor visual acuity of human surveyors in low light levels, even when utilising acoustic equipment, occupancy of roosts such of this (and, indeed, any woodland roost of late-emerging species) can be difficult to confirm without the use of infrared or thermal imaging equipment. We posit that, until recently, the reliance of unassisted surveyor observations and the lack of requirement for thermal or infra-red optics may have contributed to what is likely to be a significant degree of under-recording of this type of behaviour, and of woodland bat roosts in general. We would recommend that due to the innate poor detectability of some species both visually and acoustically (Froidevaux et al. 2020), emergence surveys should utilise night vision aids, particularly in woodland environments, as suggested in the recently published Interim Guidance on the use of Night Vision Aids for surveys (Bat ConservationTrust 2022) which should go some way to addressing this issue.

This work represents an in-depth study of two colonies of bats within a single woodland, and as such, further work is required to record and document interspecific cohabitation roosts of bats in other locations. Future work with these specific colonies comprises the long-term monitoring of each group of bats through a ringing scheme which began in 2021. It is hoped that the re-capture of bats from these colonies in future years may provide further insight into the movements and interactions of these colonies, determine whether the interspecific cohabitation observed in this study is indeed that of returning colonies of the same bats each year, and provide a detailed understanding of the fission-fusion behaviour of woodland bats.

ACKNOWLEDGMENTS

REFERENCES

ALTRINGHAM, J. D. (2003). British bats. ed.: Harper Collins. London, UK, 218 pp.

ANDREWS, H., PEARSON, L. & BUTT, L. (2017). A review of empirical data in respect of emergence and return times reported for the UK's 17 native bat species. ed.: AEcol. Bridgwater, UK, 34 pp.

ANDREWS, H. & GARDNER, M. (2015). Surveying trees for bat roosts: encounter probability v. survey effort. *In Practice*, 88: 33-37.

ANDREWS, H. (2020). Bat tree habitat key. 4th edition. ed.: Andrews Ecology. Bridgwater, UK.

AUGUST, T. A., NUNN, M. A., FENSOME, A. G., LINTON, D. M. & MATHEWS, F. (2014). Sympatric woodland *Myotis* bats form tight-knit social groups with exclusive roost home ranges. *Plos One*, 9(10): e112225. https://doi.org/10.1371/journal.pone.0112225

BARLOW, K. (1999). Expedition field techniques. Bats. ed.: Royal Geographical Society with IBG. London, UK, 69 pp.

BARRETT-HAMILTON, G. E. H. (1910). A history of british mammals. Vol. I. - Bats. ed.: Gurney and Jackson. London, UK, 371 pp.

BAT CONSERVATION TRUST. (2022). Interim guidance note: use of night vision aids for bat emergence surveys and further comment on dawn surveys. ed.: Bat Conservation Trust.

BIKOS, K., BRASTAD, I., BUCKLE, A., GUNDERSEN, M., JONES, G., KHER, A. & REHBERGER, G. (2021). Time and date. Accessed: 10 June 2021.

BOONMAN, M. (2000). Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). *J Zool*, 251(3): 385-389. https://doi.org/10.1111/j.1469-7998.2000.tb01089.x

BTHK. (2018). Bat roosts in trees. A guide to identification and assessment for tree-care and ecology professionals. ed.: Pelagic Publishing. 264 pp.

CIECHANOWSKI, M. (2022). Community structure and activity of bats (Chiroptera) over different water bodies. *Mamm Biol*, 67: 276-285. https://doi.org/10.1078/1616-5047-00042

COLLINS, J. (2016). Bat surveys for professional ecologists: good practice guidelines. 3rd edition. ed.: Bat Conservation Trust. London, UK, 103 pp.

DAVIDSON-WATTS, I. (2003). Bat survey of Briddlesford Copse, Isle of Wight. Fordingbridge.

DAVIDSON-WATTS, I. (2021). 'Can you see what I see?' - The importance of night vision aids to conduct effective emergence surveys of tree roosting bats. In: UK Bat Steering Group Meeting. ed.: Bat Conservation Trust.

DIETZ, C. & KIEFER, A. (2016). Bats of Britain and Europe. ed.: Bloomsbury. London, UK, 398 pp.

ELEKON AG. (2019). Bat explorer software.

ENCARNAÇÃO, J. A., BECKER, N. I. & EKSCHMITT, K. (2010). When do Daubenton's bats (*Myotis daubentonii*) fly far for dinner? *Can J Zool*, 88(12): 1192-1201. https://doi.org/10.1139/Z10-085

FLEISCHMANN, D. & KERTH, G. (2014). Roosting behavior and group decision making in 2 syntopic bat species with fission - fusion societies. *Behav Ecol*, 25(5): 1240-1247. https://doi.org/10.1093/beheco/aru117

FROIDEVAUX, J. S. P., BOUGHEY, K. L., HAWKINS, C. L., JONES, G. & COLLINS, J. (2020). Evaluating survey methods for bat roost detection in ecological impact assessment. *Anim Conserv*, 23(5): 597-606. https://doi.org/10.1111/acv.12574

GIUNTINI, S., ANCILLOTTO, L., FALASCHI, M., VIVIANO, A., PALAGI, E. & MORI, E. (2022). Alien parakeets as a potential threat to the common noctule *Nyctalus noctula*. *Biodivers Conserv*, 31: 3075-3092. https://doi.org/10.1007/s10531-022-02476-9

GOITI, U., VECIN, P., GARIN, I., SALOÑA, M. & AIHARTZA, J. R. (2003). Diet and prey selection in Kuhl's pipistrelle *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) in south-western Europe. *Acta Theriol*, 48: 457-468. https://doi.org/10.1007/BF03192492

HAELEWATERS, D., PAGE, R. A. & PFISTER, D. H. (2018). Laboulbeniales hyperparasites (Fungi, Ascomycota) of bat flies: independent origins and host associations. *Ecol Evol*, 8(16): 8396- 8418. https://doi.org/10.1002/ece3.4359

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(3): 767-774. https://doi.org/10.1644/1545-1542(2002)083<0767:FDAHRO>2.0.CO;2

KERTH, G. & KONIG, B. (1999). Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour*, 136(9): 1187-1202. https://doi.org/10.1163/156853999501711

KERTH, G., EBERT, C. & SCHMIDTKE, C. (2006). Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. *Philos T R Soc B*, 273(1602): 2785-2790. https://doi.org/10.1098/rspb.2006.3647

KERTH, G. (2008). Causes and consequences of sociality in bats. *BioScience*, 58(8): 737-746. https://doi.org/10.1641/B580810

KUNZ, T. H. & KURTA, A. (1988). Ecological and behavioral methods for the study of bats. ed.: Smithsonian Institution Press. Washington, D. C., USA, 533 pp.

LAFORGE, A., ARCHAUX, F., COULON, A., SIRAMI, C., FROIDEVAUX, J., GOUIX, N., LADET, S., MARTIN, H., BARRÉ, K., ROEMER, C., et al. (2021). Landscape composition and life-history traits influence bat movement and space use: analysis of 30 years of published telemetry data. *Global Ecol Biogeogr*, 30(12): 2442-2454. https://doi.org/10.1111/geb.13397

LINTOTT, P. R., BUNNEFELD, N., FUENTES-MONTEMAYOR, E., MINDERMAN, J., MAYHEW, R. J., OLLEY, L. & PARK, K. J. (2014). City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. *Roy Soc Open Sci*, 1(3): 140200. https://doi.org/10.1098/rsos.140200

LUČAN, R. K. (2009). Effect of colony size and reproductive period on the emergence behaviour of a maternity colony of Daubenton's Bat (*Myotis daubentonii*) occupying an artificial roost (Chiroptera: Vespertilionidae). *Lynx*, 40: 71-81.

MIDDLETON, N., FROUD, A. & FRENCH, K. (2014). Social calls of the bats of Britain and Ireland. ed.: Pelagic Publishing. Exeter, UK, 176 pp.

NYHOLM, E. S. (1965). The Ecology of *Myotis mystacinus* and *M. daubentonii* (Chiroptera). *Ann Zool Fenn*, 2: 77-123.

R DEVELOPMENT CORE TEAM. (2014). R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

RACEY, P. A. & ENTWISTLE, A. C. (2000). Chapter 9 - Life-history and reproductive strategies of bats. In: Reproductive biology of bats. ed.: Academic Press. Cambridge, UK, p.363-414. https://doi.org/10.1016/B978-012195670-7/50010-2

RUCZYŃSKI, I. & BARTOŃ, K. A. (2020). Seasonal changes and the influence of tree species and ambient temperature on the fission-fusion dynamics of tree-roosting bats. *Behav Ecol Sociobiol*, 74: 63. https://doi.org/10.1007/s00265-020-02840-1

RUSS, J. (2012). British bat calls. A guide to species identification. ed.: Pelagic Publishing. India, 192 pp.

RUSS, J. (2021). Bat calls of Britain and Europe. A guide to species identification. ed.: Pelagic Publishing. Wales, UK, 462 pp.

RYBERG, O. (1947). Studies on bats and bat parasites. Especially with regard to Sweden and other neighboring countries of the North. ed.: Bokförlaget Svensk Natur. Stokholm, Sweden, 330 pp.

SALINAS-RAMOS, V. B., ANCILLOTTO, L., BOSSO, L., SÁNCHEZ-CORDERO, V. & RUSSO, D. (2020). Interspecific competition in bats: state of knowledge and research challenges. *Mammal Rev*, 50(1): 68-81. https://doi.org/10.1111/mam.12180

WELCH, J. N. & LEPPANEN, C. (2017). The threat of invasive species to bats: a review. *Mammal Rev*, 47(4): 277-290. https://doi.org/10.1111/mam.12099

WICKHAM, H. (2016). ggplot2: Elegant graphics for data analysis. New York, Springer-Verlag.

WKS SOFTWARE LTD. (2021). Lightworks 2021.3. Watertown.

WUHAN GUIDE INFRA-RED CO, L. (2019). TrackIR. Wuhan, Wuhan Guide Inrfra-red Co, Ltd.

ZEUS, V. M., PUECHMAILLE, S. J. & KERTH, G. (2017). Conspecific and heterospecific social groups affect each other's resource use: a study on roost sharing among bat colonies. *Anim Behav*, 123: 329-338. https://doi.org/10.1016/j.anbehav.2016.11.015