Automated long-term registration of bat activity at Fort Steendorp (Flanders, Belgium)

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Abstract: Fort Steendorp (east of Temse, East Flanders, Belgium) is a large former military brick fortification, which is nowadays one of the most important bat hibernation sites in Flanders. The fortification is part of two, 19th and early 20th century defensive 'belts' of fortifications around the city and port of Antwerp. Standardized winter census counts were started in 1989. From 1999 to 2022, the overall number of hibernating bats counted varied between 734 and 1209, belonging to eight species. Each year the population is made up of approximately 69% Daubenton's bat (*Myotis daubentonii*). This is by far the most abundant species, but it has been sharply decreasing in numbers. Bats can be hard to detect during hibernation, with visual census counts representing only part of the actual number of hibernating bats. In order to quantify the proportion of bats that are missed during visual counts, an automated bat count experiment was set up using an infrared light barrier system, measuring bat activity and passes in and out an enclosed part of Fort Steendorp. All year round data collection also allowed us to collect bat activity data outside the hibernation season. An important difference with the visual method is that it is not possible to determine the species with this type of automated bat survey. The paper presents the data from four consecutive years, starting from April 2014. We observed two distinct periods of high activity at Fort Steendorp. A first peak of activity (movements in and out of the infrared light barrier portal) was seen from the second half of May, going on into the first half of June (an average 1000 bat passes through the portal per night). This coincided with the spring swarming/mating season of most bat species. An even more notable increase of activity in and out of the enclosure was seen between mid-August up to October, preceding hibernation ('autumn swarming', with an average of 5000 bat passes per night). From mid-October onwards, a net movement of bats into the study zone took place, with a gradual build-up of bats going into hibernation. Between 1761 and 2066 bats were found to hibernate in the study zone. When comparing visual counts with infrared light barrier portal data, both observing the same enclosure and same study period, only 37% of the observed total bat population were detected visually. This figure indicates that around two thirds of the bats hibernate in inaccessible 'water corridors', or are tucked away in cracks and crevices, going unnoticed in a visual count. Secondly, our results show that hibernation is not a continuous uninterrupted process. From December onwards, before the coldest part of winter, bats move out of the enclosure, presumably to other parts of the fort, despite hibernation conditions in other parts of the fort being unlikely to be more favourable. We cannot say when bats start to leave Fort Steendorp, ending their hibernation season, but by the last week of March, all the hibernating bats had left the study zone, and by deduction also Fort Steendorp. There was little to no activity until the spring swarming in May and June. After this, the activity in and around the infrared light barrier dropped again to almost zero until August. This paper provides strong evidence that for complex bat hibernacula, with plenty of crevices and inaccessible or hidden shafts and corridors, the actual numbers of hibernating bat are far higher than the numbers counted visually. This has important consequences, at least for large brick hibernation sites such as Fort Steendorp, and for bat conservation efforts at sites with a high value for bats. When around 1000 bats are seen in Fort Steendorp in yearly census counts, the actual number of bats hibernating will be closer to 3000, elevating the importance of the site for bat conservation. Peak activities in sites like this in May-June and August-November lead to the conclusion that, for the optimal protection of bats, conservation measures should not be limited solely to the hibernation period.

Keywords: automated monitoring, hibernation, bat activity, underground sites, fortification.

Introduction

In temperate regions, bats need to hibernate due to a limited food supply and to conserve their energy. Studies in both the Netherlands and Belgium (Daan 1980, Dekeukeleire et al. 2011, van Schaik et al. 2015, Boeraeve et al. 2019) have shown the importance of hibernacula during autumn, spring and even summer. Most long-term bat population monitoring programmes are based upon one or more censuses of hibernating animals in hibernation sites (Daan 1980, Voûte & Sluiter 1980, Kervyn et al. 2009, Haysom et al. 2013). These annual census programmes are performed visually by counting each individual bat spotted.

During autumn, bats assemble around underground sites for swarming. Autumn swarming behaviour, prior to hibernation, is thought to primarily be mating behaviour (Saucy 2019), but may also be related to the localization and assessment of hibernacula (van Schaik et al. 2015). Different authors (Degn et al. 1995, Encarnação 2005, Furmankiewicz 2008) have also observed swarming during spring among brown long-eared (*Plecotus auritus*) and Daubenton's bats (*Myotis daubentonii*). In addition, studies with banded bats have indicated large internal migrations within marl caves (de Wilde & van Nieuwenhoven 1954, Punt 1957). It seems that bat species awake during hibernation and change their location within, or even between, hibernation sites due to slight changes of ambient temperature in the hibernaculum depending on the outside temperature (Daan 1973, Ransome 1990). In the annual bat census programmes in forts, movements of bats during autumn, spring and even summer, have rarely been taken into account and this may indicate an underestimation of the total numbers of bats and the importance of some sites for bats (Kugelschafter 1994). In addition, forts differ in their size, number of entrances and hidden spaces that are not accessible and/or not visible to humans. To date, we lack knowledge on the seasonal use of forts by bats over the whole year and how this is related to outside temperatures, especially on daily activity during the swarming period. In addition, entrance to most of the forts is only allowed by special permission from the Agentschap voor Natuur & Bos (Brussels, Belgium), due these constructions having unstable and unsafe areas. These safety restrictions can be expected to increase the missing counts; other options for monitoring bat populations and determining the importance of these forts for bats need to be investigated.

Research presented at the First European workshop on the Automatic Monitoring of Bat Roosts, held in Bad Segeberg (Germany) showed that the use of infrared light barriers enhances our knowledge about hibernacula (Jansen et al. 2014). The hidden proportion of hibernating bats has been estimated to range between 22% up to 99% (de Rue & Daan 1972, Kugelschafter 1994, Degn et al. 1995, Jansen et al. 2014).

This paper looks at year round bat activity in a closed study zone of a fort, measuring net movements registered by an automated infrared light barrier and evaluates how effective such a system is as an indicator for bat activity in a large winter hibernaculum. Additionally, we seek to compare the number of bats visually counted with those registered with an automated system. Our last topic of interest is the seasonal use of underground structures by bats over a year long period and how these are related to outside temperatures, with specific attention to daily activity during different periods of the year. The relevance of using an automated infrared light barrier system for bat conservation is also discussed.

Materials and methods

Study Site

In temperate regions, in the absence of natural caves, man-made underground structures (quarries, military forts, ice cellars, etc.) offer environmental conditions that are suitable for bat hibernation. There are 35 19th and early 20th century forts belonging to two defensive 'belts' of fortifications remaining around the city and port of Antwerp. In Flanders, as in the rest of the EU, most major bat hibernation sites are protected by national, regional and/ or EU legislation.

Fort Steendorp (51.1269°N 4.2561°E, Temse, Belgium) is one of the most important hibernation sites for bats in Flanders. The first efforts to protect bats on site go back to 1978 with an agreement between the owner at that time – the Ministry of Defence – and the Royal Belgian Institute of Natural Sciences. Standardized winter counts started from 1989. Due to the gradual closing of access to the underground structures, the population of hibernating bats increased steadily. The site received a higher status of protection as a 'natural landscape' in 1995. After being acquired by the Flemish government in 2001 it was recognized as a Natura 2000 area by the Flemish Agency for Nature and Forests.

Fort Steendorp is a large star shape brick structure built between 1882 and 1892, and covers an area of about 20 hectares. It is one of the largest military defensive structures ever built in Belgium. It is a very complex structure of brick halls, rooms and corridors, battery structures reinforced with concrete and covered by a layer of earth. The bricks used to build the structure were locally-produced traditional red fired bricks. The fort was surrounded by a dry moat, overlooking the river Scheldt, 15 km from the city of Antwerp (figure 1) (Colaes & Gils 1991, Gils 2000). Fort Steendorp was part of an EU co-sponsored LIFE-project 'BatAction' that ran from 2006 to 2011 (Verwimp 2006). The fort's design is quite different from all the others around Antwerp. Most of the other forts consist of concrete structures and a limited number of bricks, which are built above the ground. The fort has been heavily damaged over the course of history by several large explosions caused by retreating Belgian or foreign forces. Due to a lack of maintenance after 1945, the fort continued to fall into disrepair. The site evolved naturally and was partially replanted into a woodland type of environment. Over time, some of the underground chambers, corridors and service corridors became a moist, partially flooded environment making them highly suitable for hibernating bats.

Infrared light barrier data recording

The centrally located extra-fortified part of the fort ('*reduit*') was selected for this study. An automated infrared light barrier system was placed in the flight opening of the door closing off the right hand side entrance to the circular corridors of the *reduit* (in blue, fig-

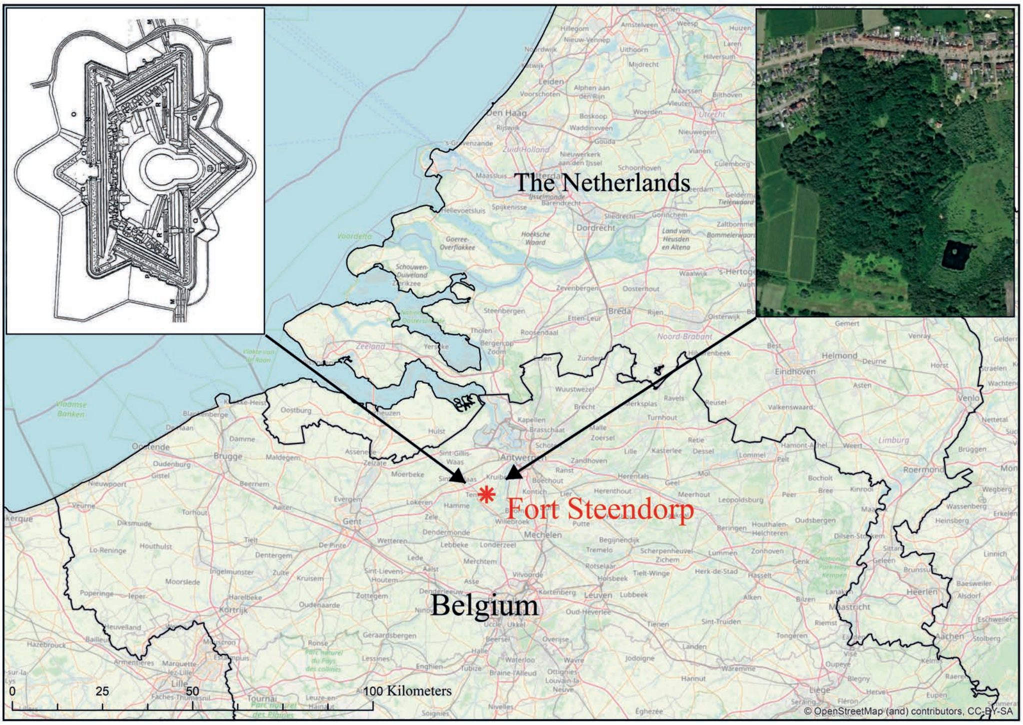

Figure 1. Location of the star shaped Fort Steendorp, Temse, East Flanders, Belgium. The fort has an outer earth walling, dry moat and brick structures. *Ground plan (upper left): ANB. Aerial photo (upper right): Google Maps 2022. https://goo.gl/maps/rg9gfRYuikDGfXyc7.*

ure 2). The left hand entrance is obstructed by debris caused by damage to the fort (in grey, figure 2). All other possible flight entrances were sealed off. This left only one point of entry to the circa 250 metres of brick corridors.

Narrow service corridors that are meant to drain water run alongside the main circular corridors. These are known as water corridors and not easily accessible for census counts. They are often partially flooded and therefore highly favourable for bat hibernation. The temperatures at the infrared light barrier and in most parts of the enclosure are 9-10 °C all year round. Temperatures in the larger hallway and the chambers of the front part of the '*reduit*' barely fluctuate in response to outside temperatures (internal: 4.5-4.6 °C vs. external: -0.2–2.4 °C) (Meermans 2004). From the yearly visual bat census, we know that between 2014 and 2017 Daubenton's bat accounted for an average 73% of the total population, with Geoffroy's bat (*Myotis emarginatus)* at 15% and whiskered and/or Brandt's bat (*Myotis mystacinus/brandtii)* on average 7%.

The infrared light barrier system was designed and constructed by Anne-Jifke Haarsma and has proven to be an efficient tool for counting bat passes in and out of sites (Haarsma 2006, Steck & Brinkmann 2015). We installed a double barrier of infrared beams mounted in a frame in a metal door at a height of 1.6 metres. Each barrier encompassed two parallel rows of twelve infrared light transmitters linked to 24 photoelectric receivers on the opposite side with three cm between the first and the second rows of infrared lights. The light barriers were powered by an external 12V battery, which was replaced every 2-3 weeks. The system triggers a signal when an infrared light beam is

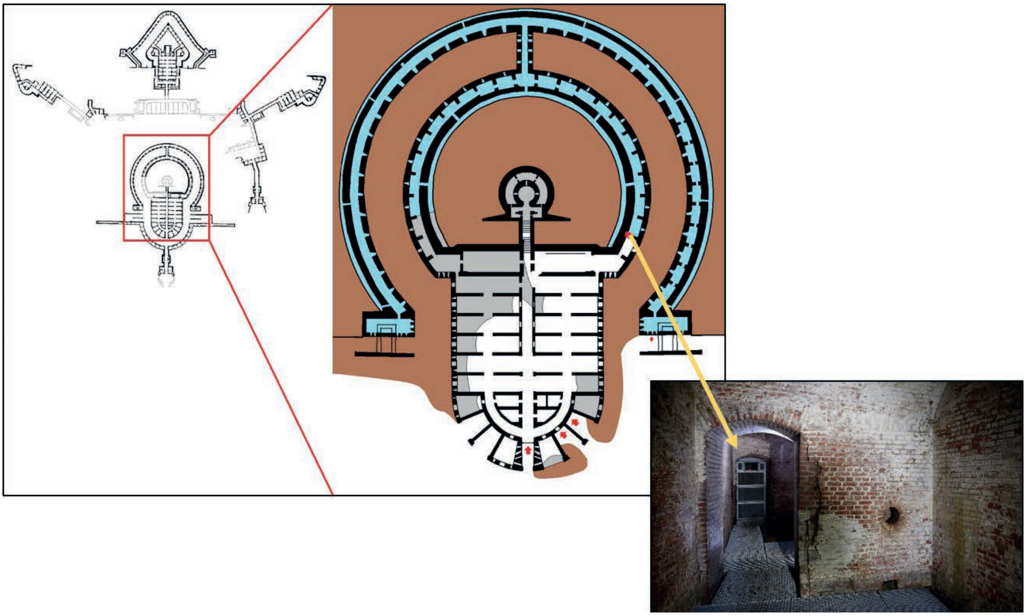

Figure 2. schematic view of the *reduit* of Steendorp Fort. The yellow arrow indicates where the infrared light barrier was placed. The blue coloured part is our study zone. The grey coloured sections are damaged and /or collapsed parts of the fort. Red arrows indicate entrances to the *reduit* that were closed off. *Source: Figure adopted from Gils (1991) by the authors. Photo: J. Goossens.*

blocked to reach the receiver. Visual observations indicate that birds do not reach the study area, which is over 50 metres from the outer entrance of the *reduit*. Moths were expected to not trigger the infra-red sequence, but if they did so, they cannot be filtered out.
The infrared light barrier recorded seven different types of signals (figure 3):

- i: one or more of the infrared light beams of the first row are blocked, without interfering with the second row of beams. Conclusion: no 'true' pass, e.g. bats were swarming on the outside of the barrier.
- I: one or more of the beams of the first row are blocked, followed by the second row of beams being blocked. The second row of beams is cleared first before the first row of beams becomes clear. Conclusion: the bat returned via the first row = no 'true' pass.
- IN: one or more of the beams of the first row are blocked and thereafter (within 0.5 sec) the second row of beams is blocked. The first row of beams is cleared first before the second row of beams becomes clear. Conclusion: a bat has passed the infrared light beam system from the outside, going in.

The same applies in reverse for bats going out from the inside (o, O and OUT; figure 3). Again the movement cycles are expected to happen within 0.5 second. For obvious reasons, the species of bat cannot be identified by this infrared method.

A last type of signal was an 'error' signal indicating that more than ten beams were blocked simultaneously, indicating a large animal passed the infrared light barrier. Slow moving animals (e.g. snails) will not be recorded.

Recordings of bat passes for this study ran during almost four consecutive years from 11 June 2014 to 10 January 2018. For the data analysis only 'true' passes (IN (= -1) and OUT (= +1)) were used. Upon eight occasions, between 24 hours up to 83 days (due to long repairs or battery failure) the times series was temporarily disrupted.

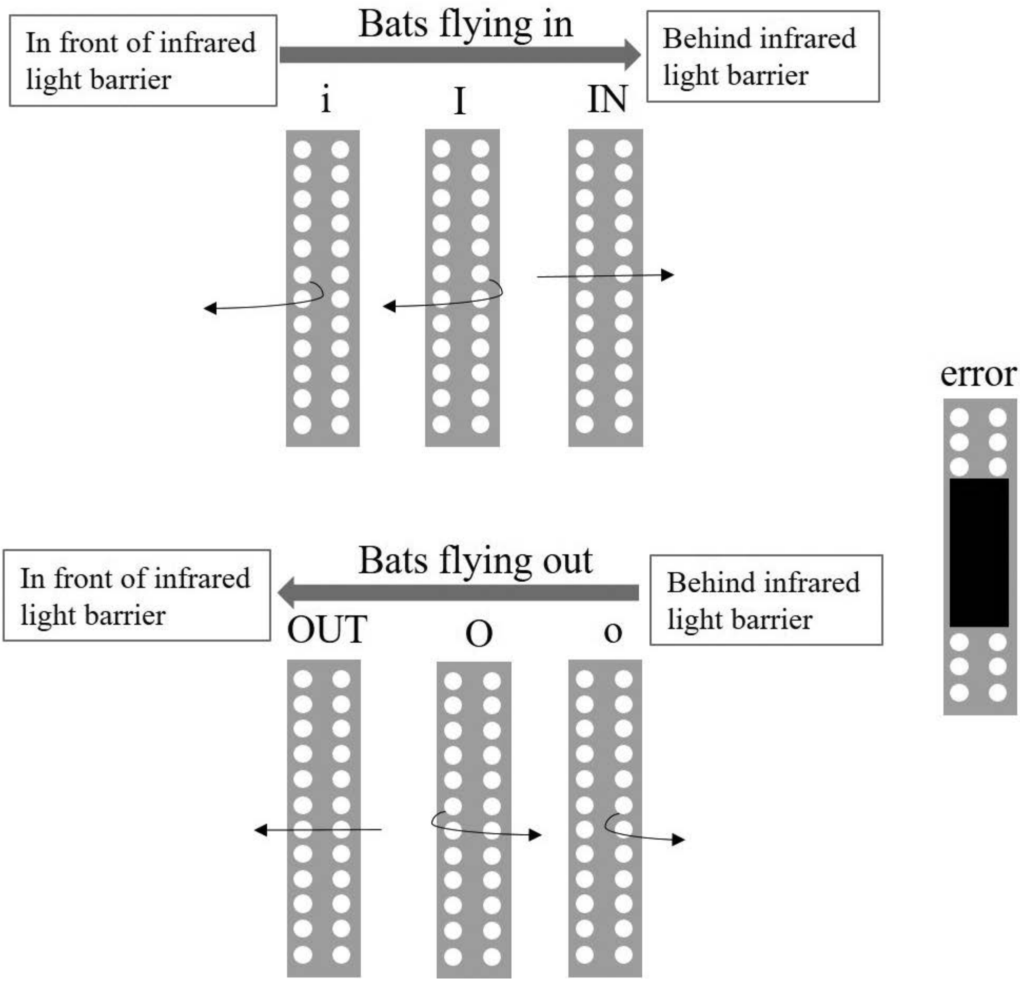

Figure 3. The seven different types of signals recorded by the infrared light barrier. The arrow indicates which row of infrared beams is blocked and in which direction the bats were flying.

We aligned our twelve months of recordings with the biological seasons, starting from 1 April up to 31 March the following year. Bat passes 'IN' and 'OUT' of the portal were used to calculate the cumulative numbers of bats remaining behind the portal at any given moment. This allowed us to see the net movement of bats moving into the *reduit*, and into hibernation. While it is possible that at any time, a small number of bats may have been in the enclosure during daytime even outside the hibernation season, the lowest number of each yearly cycle was set as the zero reading (assuming that all the bats had left the compound).

Activity Graphics were made using free software for statistical computation and graphics R version 4.1.1 and Microsoft Excel 2016.

Climate data

Climate data (daily data of the minimum and maximum temperatures in degrees Celsius) were obtained through the European Climate Assessment & Dataset ECA&D project. The closest climate data location to Temse was

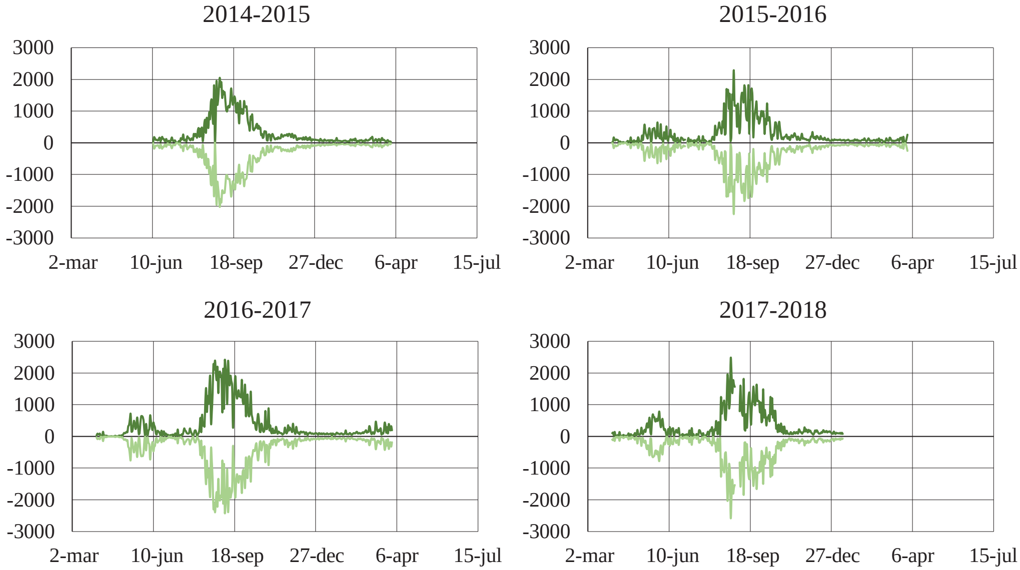

Figure 4. One-year bat activity (noon to noon; 1 April to 31 March), showing passes 'IN' (upper part of the graph) and 'OUT' (lower part of the graph) of the infrared portal. Data from June 2014 to the end of January 2018.

selected, which was Melsele, 10 km distance from Fort Steendorp.

Yearly on-site annual census counts

Since 1998-1999, between 10 to 20 well-trained bat observers from the Flemish bat-working group of Natuurpunt vzw carry out annual census counts. All accessible areas, including non-flooded water corridors, are surveyed. The location and species of each observed bat is noted on detailed maps. Due to safety concerns at the time, no census counts were carried out between 2007 and 2010 and in 2021 due to the Covid-19 pandemic. Sometimes there were difficulties in differentiating between whiskered and Brandt's bats so we have grouped these two species together.

Results

Bat passes through the infrared light barrier

From 11 June 2014 to 10 January 2018 a total of 875,385 bat movements were registered, with 431,262 (49.3%) bats passes 'IN' the closed study area, 430,073 (49.1%) flight movements 'OUT', and 14,050 'other' invalid movements (i, I, o, O, or error) (1.6%) (table 1). We aligned our data along bat 'seasons' starting from 1 April and the end of hibernation, ending the following 31 March.

Throughout the year there were two periods of high bat activity. A first peak of activity - spring swarming - was seen during the second half of May going on into first half of June, with a maximum of 1000 daily movements per night through the infrared light barrier but no 'building up' of bats staying 'behind the infrared light barrier' (figure 4). A second, much larger peak, with heavy flight activity through the infrared portal started in August, going to a maximum around the last week of August and the first week of September (autumn swarming). At maximum, up to 5000 'passes' were recorded per night (table 1). We cannot tell how many bats were involved in these activity patterns or how long the bats were active in and around the hiberna-

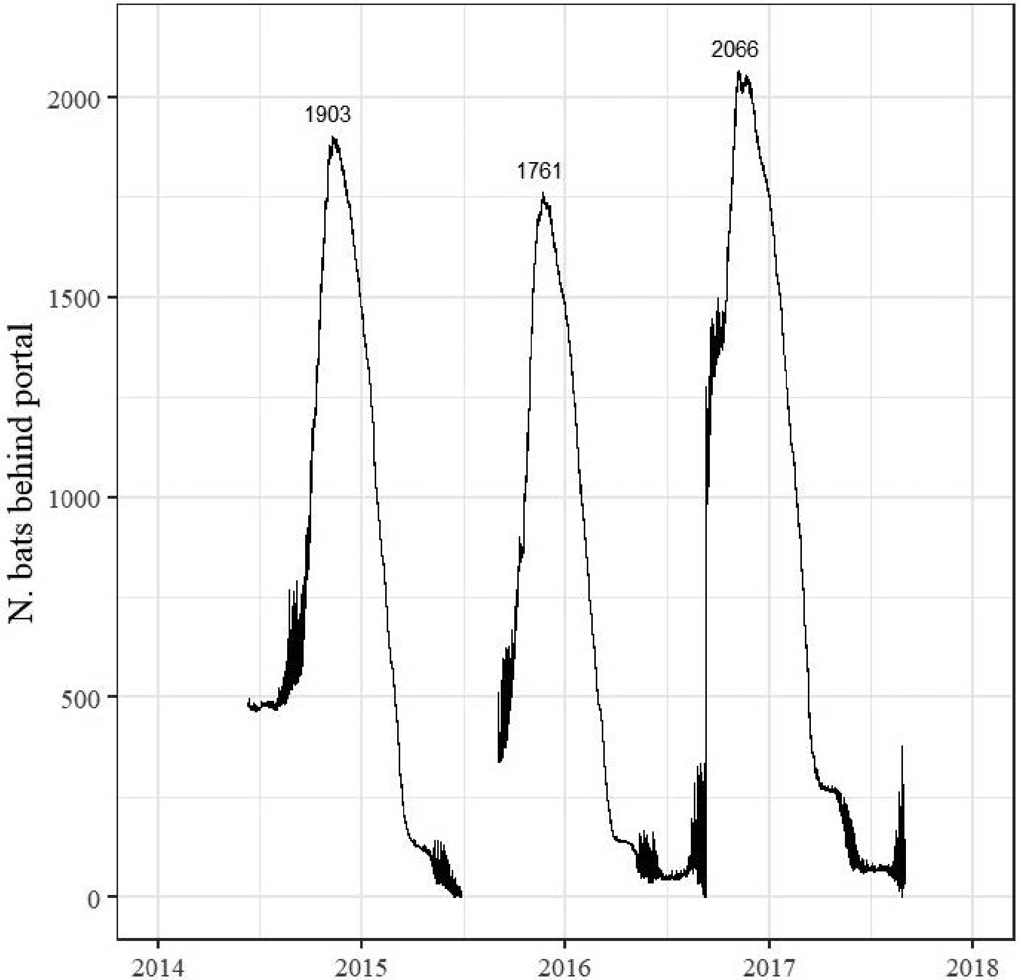

Figure 5. Number of bats behind the infrared light barrier for three continuous data sessions from April to March. The graphs are set to zero at the lowest number for each year. The highest number of bats 'behind the portal' for each winter is indicated on the graph.

tion site before going into hibernation. From the second half of September on, bat activity decreased with bats gradually going into hibernation and staying 'behind the portal'. Awakening from hibernation and leaving the site does not lead to a high number of bat passing through the portal. The bats just leave, and do not stick around.

The net movement of bats into the *reduit* starts from the second week of September, with bats staying behind the barrier and assumed to be in hibernation by the first week of November. By the end of November, most bats have moved into the *reduit*, and into hibernation.

The maximum numbers of bats 'behind the portal' varied between 1761 and 2066 (figure 5, table 1). This number is a maximum calculated from the net number moving 'IN' and 'OUT'. The maximum numbers of bats were registered during second half of November for all years.

Figure 6 compares the cumulative build-up of bats 'behind the portal' (a) and bat activity through the infrared portal in and out of the *reduit* (b) with the actual outside temperatures

Table 1. Overview of recorded IN and OUT passes by the IR (infrared) portal between 11/06/2014 and 10/01/2018.

start session	end session	IR portal passes (IN)	IR portal passes (OUT)	total passes	difference IN-OUT	max passes/ night	max *n* behind portal
11/06/2014*	31/03/2015	98,630	98,286	196,916	344	4074	1903
01/04/2015	31/03/2016	102,033	101,564	203,597	469	4539	1761
01/04/2016	31/03/2017	134,008	133,183	267,191	825	4793	2066
01/04/2017	10/01/2018*	96,591	97,040	193,631	449	5022	Incomplete**

*2014 May/beginning June swarming missed; **monitoring stopped 11/01/2018

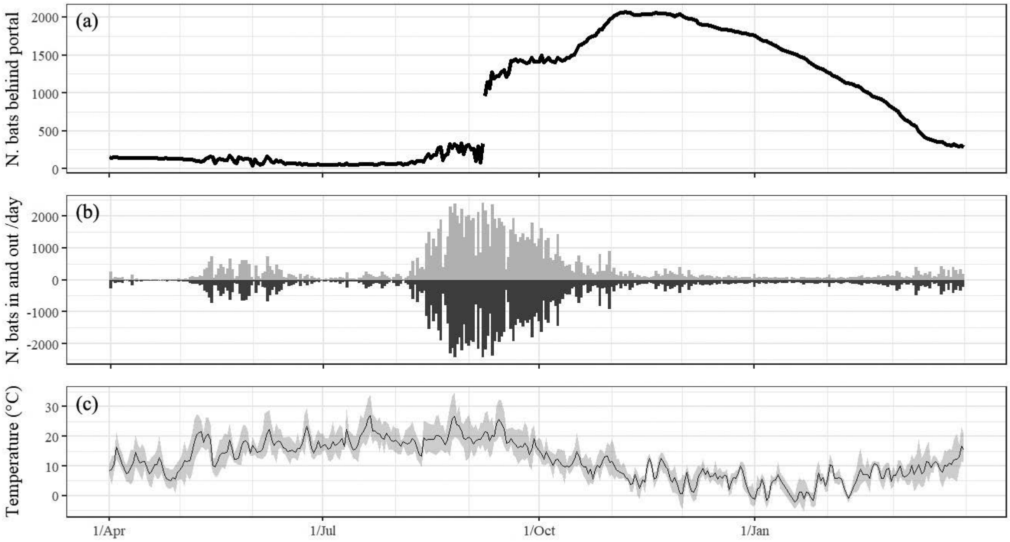

Figure 6. The cumulative build-up of bats 'behind the portal' between 1 April 2016 and 31 March 2017. From top to bottom: a. Number of bats behind the infrared light barrier; b. 24-hour activity in (grey) and out (black) of the infrared portal; c. Outside temperature measured at the weather station of Melsele, 10 km from the study site.

(c) for the 2016-2017 season. The net movement of bats into the *reduit* coincides with the gradual decrease of the outside temperature, leading to a maximum number of bats 'behind the portal' at the end of November. However, even at the moment when it is generally assumed that bats are in hibernation, the flights through the portal did not stop. Throughout the month of January, on average 20 bat passes were recorded in and out of the flight opening leading to the study zone.

Even more striking is that bats start moving out of the stable environment of the *reduit* area as early as the end of December: a month before the coldest part of winter. By February, half of the hibernating bats had already moved out of the *reduit* enclosure, probably relocating towards the entrance of the fort. More or less all the bats had left the '*reduit*' (and maybe the fort) by the end of March. There was little to no activity until the activity peak of May/June.

The population of hibernating bats at Fort Steendorp, a comparison of counting methods

We also looked at overall numbers of bats hibernating at Fort Steendorp. Figure 7 shows

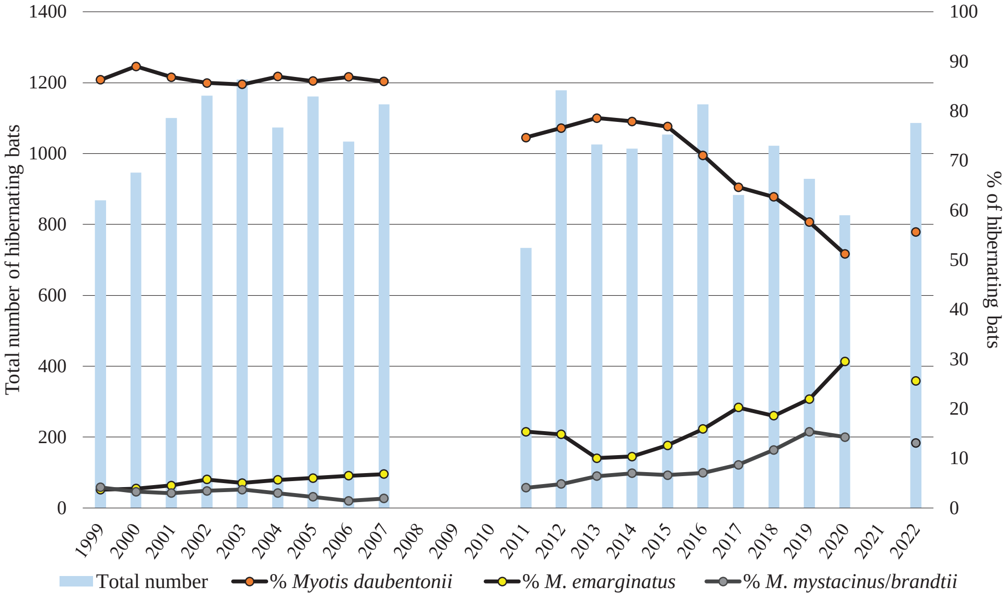

Figure 7. Total number (left axis) and proportion (% right axis) of hibernating bats in Fort Steendorp (entire fortress) since the winter of 1998-1999 and the three most abundant species: Daubenton's bat, Geoffroy's bat and whiskered and/or Brandt's bat. Data: Natuurpunt vzw bat working group. Due to safety concerns, no winter counts were carried out from 2007-2008 to 2009-2010 and in 2020-2021 due to the covid-19 pandemic. 2010-2011 = incomplete count.

the result of a longer term series of annual bat census counts between 1999 and 2020, for the whole of Fort Steendorp; the total numbers vary from 734 to 1209. Due to security concerns, no counts were carried out during three seasons (2007-2008 till 2009-2010), as well as the 2020-2021 season, due to the Covid-19 pandemic. The 2010-2011 season was an incomplete count. Up to the winter of 2006-2007, annual census counts were done in mid January; since 2010-2011 they have been performed during the weekend closest to 15 February.

In total ten different species have been found hibernating in Fort Steendorp. These main species found are Daubenton's bat, Geoffroy's bat, Natterer's bat (*Myotis nattereri*) and whiskered and/or Brandt's bat. Pond bat (*Myotis dasycneme*), brown long-eared bat, grey long-eared bat (*Plecotus austriacus*), common pipistrelle (*Pipistrellus pipistrellus*) and serotine (*Eptesicus serotinus*) each represent less than 1%. Nathusius' pipistrelle (*Pipistrellus nathusius*) and noctule (*Nyctalus noctula*) have been recorded hunting in the fortress, but so far do not hibernate on site.

One of our goals was to try to evaluate how to compare bat census counts with actual numbers of bats hibernating in this type of hibernaculum. For this, we compared the bats counted 'behind the door with the infrared portal' with the data collected from the automated system. From the literature, and from personal experience, we know that the hidden proportion of hibernation bats varies greatly depending on the type of site (de Rue 1972, Kugelschafter 1994, Degn et al. 1995, Jansen 2014, Weinreich 2022). Visual annual census counts in the month of February in the *reduit* area varied from between 271 in 2015 to 340 in 2017 (table 2). Over the same time period, the cumulative data of bats 'behind the portal' varied between 703 and 991. On average, only 37% (a ratio of 2.7) of hibernating bats

Table 2. Comparison of the total number of bats behind the automated infrared portal and a standard on site visual count, at the given census date in February.

hibernation season	date of comparison	bats behind the portal	same zone manual count	%	ratio
2014-2015	15/02/2015	703	271	38.5	2.6
2015-2016	21/02/2016	621	252	40.6	2.5
2016-2017	18/02/2017	991	340	34.3	2.9
	mean	772	288	37.8	2.7

'on site' are actually detected during in visual census counts. A major reason for this is that large numbers of bats are probably tucked away in the flooded water corridors or in hollow spaces in between walls, which are inaccessible to the bat workers.

By deduction, with the latest numbers of around 1000 bats counted during the annual censuses in Fort Steendorp, the actual number is probably closer to 3000, making the site even more important for bat conservation than previously thought. This 2.7 factor does not necessarily apply to other man made or natural underground hibernation structures.

Bat activity over 24 hour periods (noon to noon)

We also looked at the activity patterns in relation to the time of night and day. Our infrared portal was 50 metres deep into the complex. In the absence of daylight and other influences from the outside world, it seemed interesting enough to find out if there were peaks in bat flight activity, and if so when. A closer data analysis showed that at some points in the year up to 5000 bat passes were recorded over one night (during autumn early swarming), during which, at peak moments, up to 600 bats passes were recorded in a single hour.

Figure 8 shows different 24-hour activity patterns (noon to noon) for some single chosen dates during the survey period (2015 to 2018), depending on the period of the year. These were: A. The end of May with spring swarming. B. The end of August at the begin of autumn swarming. C. The end of October, at the end of autumn swarming. D. The beginning of January when bats are supposed to be in hibernation.

During spring swarming (May) activity through our portal tended to be highest from 10 pm to 7 am, peaking between 3 and 5 am. At the beginning of August, portal passes started at sunset (10 pm), peaking towards 2 to 5 am with up to 400 bat passes per hour, although bat flight activity stretched well into the next day: 12 pm and even 2 pm. A different pattern was seen at the end of October, with flight activity only between 9 pm and 5 am. In the middle of the hibernation period (end of January) smaller activity patterns were also spread over the whole day, and not linked to outside diurnal rhythms.

Discussion

Census surveys of bats in hibernacula are typically performed by direct count of visible bats, using torches, headlights and a lot of effort. Site-specific underrepresentation of the true numbers of hibernating bats is likely, and is likely to vary according to the internal characteristics of each site (e.g. size, number of cracks and crevices, inaccessible tunnels etc.). Different techniques have been used to estimate the total number of hibernating bats: e.g. mark and recapture method with banded bats, passive integrated transponder PIT tags readers, genetic testing, radar beam (Punt 1957, Kugelschafter 2009, Jansen et al. 2014). Automated systems using infrared light

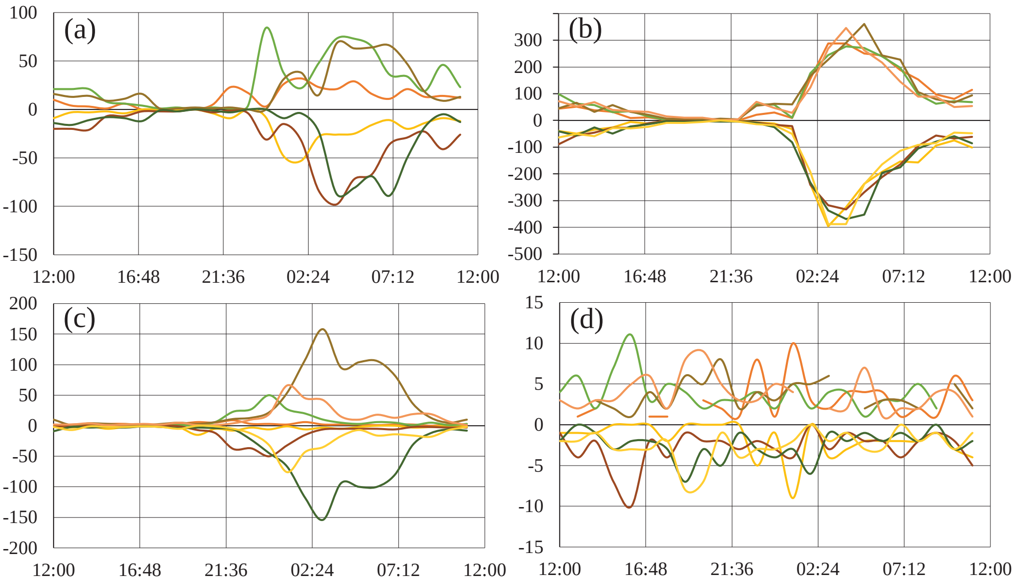

Figure 8. 24-hour activity, noon to noon the next day, for different consecutive years. a. 25 May (spring swarming); b. 29 August (beginning of autumn swarming); c. 29 October (end of autumn swarming); d. 8 January (bats in hibernation). N.B. The scales of the Y-axes differ.

beams have been applied for over fifty years (Daan 1970, Berková & Zukal 2006, Jansen et al. 2014, Kugelschafter 2014, Weinreich 2022) bringing new insights on the value of some hibernacula for bats. Based on long term data, research pioneers, such as Punt (1957) and Kugelschafter (2009), showed that the difference between counted versus actual numbers of hibernating bats can be considerable (even up to 90%) due to the existence of invisible bat 'reservoirs' in hibernating quarters.

Most studies using infrared portals monitor activities and the numbers of bats in hibernation at the entry points to forts and caves (de Rue & Daan 1972, Daan 1973, Kugelschafter 2009, Steck & Brinkmann 2015, Weinreich 2022). Only the study of de Rue & Daan (1972) at the ice cellar of Middenduin, the Netherlands, made recordings both at the entrance and further down the corridor, allowing an estimation of the direction of the winter movements from the rear to the entrance.

This study monitored activity and hibernation patterns over a four-year period, using an infrared light barrier system at the entrance of a favourable and totally enclosed part of Fort Steendorp. The door with the monitored flight opening is the only way into the study zone, the *reduit* of the fort. We limited the chance that bats entering the same zone would be 'missed' by blocking off the other entry points. Different visual observations suggested that the infrared portal in the flight opening of the door to the *reduit* did not seem to have any influence on bats entering the zone. Comparing the visual counts and those from the infrared portal allows us to come up with a more accurate estimate of how many bats actually hibernate in Fort Steendorp. We know that 'invalid movements' on account average for only 1.6% of registrations. This number is low, and not unexpected when, at some moments, 600 bat passes were registered in an hour.

Activity patterns and hibernation

Our study shows high spring activity peaks through the infrared portal leading to the *reduit*, in May into June, and an autumn activity starting mid-August with bats are assembling and getting ready to go into hibernation. No building up of bats 'behind the portal' takes place at that moment. From the end of September, the number of bats flying in but no longer coming out of the study area builds up, reaching maximum numbers by the end of November. From visual observations, we know that by then, most bats are in hibernation. From on-site observations, we know that by the end of March most hibernating bats have left, with the exception of some Geoffroy's bat that tend to remain on site into the first half of May.

In 1932, the observation that large numbers of bats visit caves and mines in autumn, few months before hibernation, was first described by Poole in North America and termed "swarming" (Saucy 2019). Different hypotheses have been put forward for this phenomenon: assessing suitable hibernacula and introducing juveniles to hibernation locations, but the most common explanation is that swarming is considered as a mating event (Saucy 2019). Swarming occurs at night; the first individuals usually arrive sometime after sunset and show a peak of activity between 4–6 hours after sunset (Rivers et al. 2006). The activity then gradually decreases until 4 am. Most of the swarming occurs in late summer and autumn.

In most cases, swarming is observed from mid-August to mid-November, peaking between mid-September to mid-October (Rivers et al. 2006, Saucy 2019). Encarnação (2005) did similar observations showing that young males accompanied adult male Daubenton's bats entering hibernacula from mid August until mid September to get to know their mating places. Some bats also visit more than one hibernaculum per night, which might explain the considerable night-to-night variation in activity (Humphrey & Cope 1976). However, swarming during spring has been highlighted for brown long-eared bat (Furmankiewicz 2008) and for Daubenton's bat (Encarnação 2005).

Bats stay in hibernation in high numbers during November and December, but even then, there is still a limited activity of bats moving in and out of the portal. Remarkably, bats already started to move out of the zone behind the infrared barrier during the second half of November. We do not know where the bats relocate to, but we may assume that with low outside temperatures, most bats relocate within the underground structures of Fort Steendorp. Similar events have been described for ice cellars, limestone quarries and natural caves (de Rue & Daan 1972, Daan 1973, Berková & Zukal 2006).

The cumulative numbers of bats 'behind the portal' in this study were set to zero once every season (April to March the following year) in order to estimate the total numbers going into hibernation, and to correct for small inconsistencies in the cumulative numbers that arise gradually. These inconsistencies might result from small errors in the recordings of 'IN' and 'OUT', but are also related to the enclosure never being empty at any moment in time. Very small numbers of bats will use Fort Steendorp as a temporary or permanent roosting site in the summer as well, as indicated by the all year activity patterns..

There were very small differences between bat passes 'IN and 'OUT, with resp. only 0.3, 0.5 and 0.6% more bats moving inwards (table 1). Some bats might not have left by March 31, some might have perished through predation or death. In order not to accumulate these discrepancies, curves were set to zero every year at the lowest point in June. Two, three and five day gaps in the recordings at the end of June and August 2015, and August 2017 do not influence in any way maximum numbers hibernating 'behind the portal'.

We recorded movements and passes of bats during the entire winter, indicating that hibernation is not a continuous process. Previous studies showed that in a great number of cases, spontaneous awakening occurs (de

Wilde & van Nieuwenhoven 1954). The average sleeping period is 12-14 days; although the lengths of the sleeping periods of different species of bats differ. Repeated censuses by the Flemish bat working group of hibernating quarters towards the second half of winter, show that individual bats had moved from the locations that they previously occupied. Based on banding experiments De Wilde & van Nieuwenhoven (1954) concluded that bats show a high fidelity to their hibernation quarters, but some specimens are only present during a certain part of the winter. They found that individuals of some species disappear, sometimes without being replaced and sometimes being replaced by individuals of a different species.

An important element to take into account is the location of the infrared light barrier, half way in the hibernation quarter, more or less 50 m from the main entrance of the site. Berková (2006) found a significant positive relationship between the number of bat passes, measured by an infrared light barrier, and the mean outside temperature at the entrance of a cave. Ransome (1990) showed that European bats do leave the caves they hibernate between December and February, mostly in low numbers, in the order of 0.5% per day. Interestingly, many outward flights were immediately (within one minute) followed by inward flights (Daan 1970). However, the number of flight movements inside the hibernating quarters during the same hibernating period were at least ten times higher (Daan 1970). In addition, studies with banded bats indicated large internal migrations within marl caves (de Wilde 1954, Punt 1957). It seems that bats awake during hibernation and change their location within or even between hibernation sites due to slight changes of the ambient temperature in the hibernaculum, linked to outside temperature conditions (Daan 1973, Ransome 1990).

Daan (1973) showed that bat populations in limestone quarries rapidly increased from the middle of September to the middle of November, although the number of Daubenton's bat continued to increase at a slower rate until the middle of January. During warmer periods bats relocated to the front part of the limestone quarry or left the site altogether. In Fort Steendorp, changes in the outside temperature are slowly reflected in the inside temperature after, on average, six days (Meermans 2004), which can trigger bats to interrupt their winter torpor. De Bruyn et al. (2021) found that hibernating bat populations use warmer parts of the system as winter progresses.

When outside temperatures start rising by the end of February, hibernating bats started moving out of the zone behind the IR barrier. By the end of March, more or less all bats had left the '*reduit*' (and maybe the fort), with exception of some Geoffroy's bats, the second most common species in the fort. This could explain why some flight activity was also seen in April. On-site observations (A. Lefevre, personal observations) showed that some Geoffroy's bats remained in their hibernating quarter up to early June.

It is unclear if the higher activity peak in May-June is linked to foraging, swarming or other patterns and it cannot be excluded that this is contributed to Geoffroy's bat coming out of hibernation. A study performed by Kugelschafter (2014) on a limestone cave in Bad Segeberg, Germany, found what was called 'springtime visits'. In this study, species identification was based on video sequences showing large clusters of adult male Daubenton´s bats entering the cave during spring. This has also been described by Degn (1989) and Harrje (1994).

Comparison with visual counts

Research presented at the First European Workshop on Automatic Monitoring of Bat Roosts in 2014 at Bad Segeberg, Germany showed that the use of infrared light barriers improves our knowledge about hibernacula (Jansen et al. 2014). The hidden proportion of hibernation bats is estimated to range between 22% to 99% (de Rue 1972, Kugelschafter 1994, Degn et al. 1995, Jansen et al. 2014).

A drawback of infrared light barrier systems is that the species flying through the system cannot be identified. However, our main goal was to get a year-round overall assessment of the activity of the total number of bats active in the fort. Species composition and the number of each species present on site are already known, based on captures during swarming and annual census counts. Dekeukeleire et al. (2011) performed a netting experiment at Fort Steendorp during three nights between mid-August and the end of September. Most of the captured individuals were Daubenton's bats (85-95%). It is worth mentioning that no maternity colonies have so far been found in Fort Steendorp.

February visual census counts show a significant decrease (35%) in the numbers of Daubenton's bat: 604 were counted in the 2021-22 season, compared to a stable average of 931 prior to 2007. Despite investments and a sustained high level of management, the number of hibernating Daubenton's bat at Fort Steendorp dropped by a third. We cannot put a finger on the reason for this decline, but likely reasons are chronically poor surface water quality, and the relentless felling of trees in the area that are suitable for this tree-dwelling species. In contrast, the numbers of Geoffroy's bat, whilst lower, are on the rise from n=58 (mean of nine years prior to 2007) to n=278 in the 2021-22 hibernation count. The rise of Geoffroy's bat seems to result from an overall increasing population, which runs parallel to a growing number of summer colonies. The numbers of whiskered and/or Brandt's bats counted hibernating at Fort Steendorp have also increased lately, from n=31 (mean of 9 years prior to 2007) to n=142 in 2021-2022). Based upon visual counts in February, Geoffroy's and whiskered and/or Brandt's bat, have seen an almost fivefold increase in numbers in the last 15 years or so.

Our extrapolation factor of 2.7 (37% of bats visible) differs from the factor of 1.2 found by Jooris & Goossens (1980) in February 1978 that was calculated from a mark-recapture experiment at the same site. Over five months they marked a total of 162 hibernating bats (142 Daubenton's bats) with small stickers on the head. The proportion of marked animals sighted after a one month varied considerably over the winter season, with 34% and 39% of the total number of sighted bats marked respectively in November and December, increasing to 52% in January and 82% for February, and (on a smaller sample size) 80% in March. During the five 'recapture' moments 15-20 bats were selected, and checked for a marking on the head, irrespective of the total number of bats present. However interesting the study is, it is not a valid mark-recapture, because the bats, being in hibernation, do not move around at random. Some probably do not move at all, or do not move during a given month. The system is also not closed, bats move in and out.

What our method measures is the fraction of visible bats against the total number present. In doing so, we also measure the fraction of bats 'in hiding' in February. What Jooris & Goossens (1980) measured is how many unmarked bats shifted place in one month, or more specifically came out of hiding or arrived from elsewhere. In November 1977, 15 bats were sampled. Nine unmarked bats came into sight, six bats were marked but we do not know how many marked bats left or moved into hiding. February 1978, 20 bats were sampled, four unmarked bats came into sight, 16 of the bats were marked but again we do not know how many marked bats left or moved into hiding. The percentages used in this 1980 publication to extrapolate for total numbers are therefore dubious. As to the conclusions on the possible 'coming out of hiding' of bats, it shows that there is more such activity in November and December than in February.

Similar research performed in an ice-cellar (Middenduin, the Netherlands) on the activity of hibernating bats with infrared sensors showed that the bat population present was two to three times higher than the on-site censuses numbers (de Rue & Daan 1972). Other studies with infrared light barrier systems in (marl)caves showed that, depending on the site and its characteristics, the censuses capture between 20 and 50% of the actual bat population (Weinreich 2022), 20% (Berková & Zukal 2006), or even less than 10% (Kugelschafter 2014). If our figure of 37% is scaled up to the censuses of the entire Steendorp Fort, the real number of hibernating bats would be closer to 3000 instead of the average 1016 bats counted over the ten last winter seasons. This could have an impact on the evaluation and reporting of overall bat numbers in Flanders, Belgium. This factor of roughly one third may apply to similar historical red brick underground structures.

Census counts at Fort Steendorp are now standardly performed in February, while the numbers in hibernation in the enclosed and, for bats highly favourable, *reduit* of the fort, peak from November to the beginning of December. By the 1st of February, over half of the bats had left the enclosure (2017 portal data, peak November *n*=2066, mid February *n*=991). It is unclear what this means for overall numbers hibernating at Fort Steendorp, whether or not the estimated 1075 bats that left the enclosure are included in the overall census count of February, or if they left for other places. In conclusion, we are sure that a correction of 37% or thereabouts should be applied to the number of bats visually counted in February. We cannot, however, ascertain whether a visual count in November would yield markedly higher numbers of bats. If so, again this would have implications for the overall estimate of bats hibernating at Fort Steendorp. However, repeated census counts at the equally important fortifications of Brasschaat and Oelegem show that two or more counts during the same winter usually show a difference of around just 10%, occasionally going up to 20% in both directions (Natuurpunt bat working group, unpublished data).

Conclusions

This study underlines the importance of man-made underground structures, such as Fort Steendorp, providing hibernacula for underground-dwelling bat populations in regions with few or no natural caves. Based on our data gathered by an infrared portal, we conclude that, at least, for the *reduit* study site and, by deduction, for the entire brick fort, the numbers of hibernating bats deduced by on-site census counts have to be multiplied by a factor of at least three. This factor coincides with earlier findings, will roughly apply to all similar structures and should not vary within the deep winter season.

The study reveals in detail the main swarming seasons for bats at Fort Steendorp (the end of May – beginning of June, and from the end of August to the end of October) and how the number of bats going into hibernation gradually builds up behind the portal, with a maximum number reached in the first half of November. Even then, a low level of flight activity is seen in and out of the enclosure. By December, even before the coldest part of winter, some bats already move out of the protective environment of the deeper *reduit*, most probably to other parts of the fort.

Even given the underestimation of hibernating bats from censuses, and in stark contrast to the trends for other species, Daubenton's bat is in sharp decline at Fort Steendorp, as in the rest of Belgian Flanders. This should trigger awareness about the ongoing logging of trees with cavities and the overall quality of surface waters, both of which are important for this species.

Our results, combined with previous studies, show that protective measures for bats at forts like this should not be limited to the mid-winter season. Clearly, Fort Steendorp is important for populations of bats all through the year. Management plans should be adopted likewise. This should include stricter criteria when repurposing important bat hibernation sites and the extension of the non-disturbance time for major parts of hibernacula from September to the end of May.

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