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Spatial and temporal variation in maternity roost site use of common pipistrelles *Pipistrellus pipistrellus* (Mammalia: Chiroptera) in Rotterdam

Tis Voortman [1,2] **& Garry Bakker** [2]

[1] Plant Ecology and Nature Conservation, Wageningen University & Research, Droevendaalsesteeg 4, 6708 PB Wageningen, the Netherlands

[2] Urban Ecology Research Unit, Natural History Museum Rotterdam, Westzeedijk 345 (Museumpark), 3015 AA Rotterdam, the Netherlands

ABSTRACT

The global trend of urbanization has a negative impact on biodiversity, but affects organisms in a species-specific way. Common pipistrelles *Pipistrellus pipistrellus* have adapted successfully to (sub)urban areas and nowadays generally find their roost within man-made structures. Nevertheless, they experience threats from urbanization, especially due to the urge to improve thermal insulation of houses, a process during which many existing and potential roosts disappear in The Netherlands. Increasing the knowledge on pipistrelle behaviour at roost sites is important to improve protective measures that are taken prior to renovation and demolition works, and therefore essential for pipistrelle conservation. Moreover, newly acquired knowledge may benefit construction of bat-friendly buildings. In this study, we monitored two pipistrelle maternity colonies for 11 weeks in a pipistrelle-rich city (Rotterdam, the Netherlands). Main objectives were to describe phenology and spatial and temporal variation in maternity roost site usage. The use of a high-resolution thermal video camera herein provided unique insights in specific behaviour of this species. Our results show that just a single building or building complex already provides plentiful space for an entire maternity colony throughout the maternity period (April-July). Individuals in both maternity colonies frequently switched to new roost openings within the same building (complex). An often assumed preference for sun-lit or indoor-heated parts of buildings was not found. Both maternity colonies were already established from April onwards, considerably earlier than generally assumed. Pipistrelle emergence behaviour related to daylight, with an optimal moment of emergence at 36 minutes after sunset. Average onset of emergence was 17 minutes after sunset, and appeared to be earlier under lower wind speed or higher temperature conditions outside the roost. Average end of emergence was 55 minutes after sunset, with mean duration of the process being 35 minutes. Duration length was not related to the total number of bats emerging, showing that pipistrelles emerge faster when more individuals are to leave from the same opening. Bats often emerged in small clustered groups within a time frame of only a few seconds. Clusters were also sometimes formed by joining passing individuals from adjacent openings. Our study provides detailed insights into the behaviour of pipistrelles during the maternity period, particularly with respect to roost utilization and emergence timing. Moreover, our study challenges certain

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Author for correspondence
T. Voortman
tisvoortman@gmail.com

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assumptions that currently serve as guidelines for taking protective measures. Ultimately, our results contribute to the knowledge on common pipistrelle conservation and suggest that alterations to current standard protocols are needed to safeguard their persistence in anthropogenic landscapes.

Keywords behaviour, high-resolution thermal camera, phenology, thermal insulation, urban ecology

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INTRODUCTION

Urbanization puts an ever-increasing pressure on natural ecosystems, which are quickly replaced by streets and buildings (Baker & Harris 2007, Grimm *et al.* 2008). This severe land use change is well known to have detrimental effects on many plant and animal species (McKinney 2008). However, there is also growing awareness of the potential that cities can have for biodiversity (Savard *et al.* 2000, Wilby & Perry 2006, Kowarik 2011, Schilthuizen 2018). So-called 'synurbic' species show a surprising ability to adapt to specific conditions of urban environments (Luniak 2004). Some species even occur in higher densities in urban areas than in their native natural habitat as they are more successful in these new environments (Francis & Chadwick 2012). European examples of synurbic species include the European fox *Vulpes vulpes*, blackbird *Turdus merula*, magpie *Pica pica*, wall-rue *Asplenium ruta-muraria* and Asian tiger mosquito *Aedes albopictus*, as reviewed by Francis & Chadwick (2012).

Bats make up a significant part of the biodiversity on earth: with at least 1386 species recognized they comprise more than $^{1}/_{5}$th of all mammal species in the world (Burgin *et al.* 2018). Nevertheless, they are also among the least studied groups of mammals. For more than half (57%) of all bat species, population trends are unknown (IUCN 2020). Of the remaining 43%, which have known population trends, half (22% of total) is decreasing. An increasing human population and associated natural habitat destruction and modification are recognized as major threats for the survival of many bat species (Hutson *et al.* 2001). However, the response of bats towards urbanization is highly species-specific, and some species have been able to successfully adapt to urban areas. A few species are even more abundant in urban environments than in other habitats, and can be considered synurbic species (Jung & Kalko 2011, Russo & Ancillotto 2015, Voigt *et al.* 2015). Where certain species use cities only for a specific activity, like roosting or foraging, for others, cities fulfill all needs and can therefore completely replace the original habitat. Often, urban structures in some way resemble natural structures. Tall buildings resemble cliffs, open attics can function like caves and a pond or swimming pool can provide fresh water all year round. Otherwise, certain city attributes may be new to bats, such as excessive lighting, traffic and pet animals, and could form a problem (Ancillotto *et al.* 2013, Medinas *et al.* 2013, Mikula *et al.* 2013, Stone *et al.* 2015). Alternatively, some bat species may adapt to such new features and make smart use of them. For example, artificial light pollution generally is a threat for bats (Stone *et al.* 2015), but it has been shown that several species use the area around street lights as foraging sites as they attract high numbers of insects (Furlonger *et al.* 1987, Rydell & Racey 1995, Gaisler *et al.* 1998, Rowse *et al.* 2016). As any small crevice in a building resembles a natural crack, urban environments provide many opportunities for roosting bats (Kunz 1982). Urban roosts can be advantageous over natural roosts due to their warmer microclimate, reducing thermal costs, accelerating pregnancy and increasing growth of juveniles (Kerth *et al.* 2001, Lausen & Barclay 2006, Voigt *et al.* 2015).

The common pipistrelle *Pipistrellus pipistrellus* SCHREBER, 1774 (hereafter: pipistrelle) is one of the most common bat species in Europe. It can be found in all European countries except for some parts of Northern Scandinavia and Russia, and its occurrence extends east to China (Mayer & Von Helversen 2001, Hulva *et al.* 2004, Niethammer & Krapp 2014). In The Netherlands, it is by far the most widespread bat species, being abundant in all parts of the country (Broekhuizen *et al.* 2016). Pipistrelles are insectivorous, feeding mainly on Diptera that are caught by aerial hawking (Barlow 1997). They hunt in a range of habitat types, like over water, in parks, in woodland, over farmland and in urban and suburban areas (Swift *et al.* 1985, Rydell *et al.* 1994, Kapteyn 1995, Vaughan *et al.* 1997, Russ & Montgomery 2002). As they evolved to forage with high manoeuvrability along tree lines and edges of forests, their wings and echolocation frequency are well adapted to foraging in urban areas with similar 'edge terrains' (Norberg & Rayner 1987, Russo & Jones 2002). Pipistrelle roosts are predominantly found in man-made structures (Kunz 1982). During the year, different types of roost sites are used, including hibernation roosts in winter, mating roosts in autumn, and maternity roosts in summer, which can all be found in urban structures (Stebbings 1968, Speakman *et al.* 1991, Park *et al.* 1998, Sachteleben & Von Helversen 2006). As this species so commonly finds its place within buildings, they are often encountered during renovation and demolition works.

Pipistrelles are protected internationally through the Bern Convention and the Eurobats agreement that resulted from the Bonn

Convention. Moreover, they are included in Annex IV of the EU habitats and Species Directive (Council Directive 92/43/EEC 1992). In most European countries, these conventions have been incorporated in national laws. In The Netherlands, the species is protected by national Nature Protection Law (Wet natuurbescherming). A protocol describes rules on how to properly study the potential presence of bats in a building (Vleermuisprotocol 2017). However, as bat behaviour has not been studied and described thoroughly, rules and laws are often based on limited observations. In recent times, an increasing number of houses in The Netherlands are insulated in order to reduce energy costs and to lower environmental impact. This nationwide renovation of buildings poses a problem for bats, as many roosting opportunities disappear when cracked walls and crevices are repaired and cavity walls are filled with insulation beads. To be able to conserve bats in cities, it is essential to learn more about their behaviour in urban areas. Newly acquired information can be used to develop bat-friendly practices in construction, maintenance and demolition of buildings and form a basis for conservation planning.

Even though pipistrelles are commonly encountered in urban settings in a major part of the world, their roosting behaviour in urban environments has been sparsely studied. A number of European studies on summer roost use have been carried out in England, Scotland and Germany (Stebbings 1968, Speakman *et al.* 1995, Webb *et al.* 1996, Feyerabend & Simon 2000, Petrželková *et al.* 2006), but similar studies in The Netherlands are scarce and rarely published. In this study, we monitored two pipistrelle maternity colonies for 11 weeks in the pipistrelle-rich city of Rotterdam, one of the largest cities in The Netherlands. The main objectives of this study were to determine how pipistrelles behave in and make use of an urban environment during the maternity period by describing phenology and spatial and temporal variation in maternity roost site usage and to identify possible consequences for bat protection measures. The use of a high-resolution thermal camera herein provided us with unique insights in specific behaviour of this species.

MATERIAL AND METHODS

Study area

The study area is the city of Rotterdam (51°55′51″ N, 4°28′45″ E), the second largest city of The Netherlands, with a population size of around 651.000 and part of an agglomeration with more than one million people. Rotterdam municipality covers 324 km^2, of which about one-third (106 km^2) is covered with water (CBS 2020). The river Nieuwe Maas divides the city in a northern and southern part. The port of Rotterdam is the largest port in Europe and extents from the North Sea coast in the west up to the city centre in the east. During World War II, the majority of Rotterdam's historic centre was destroyed when the city was bombed. As most of the city was rebuilt from the 1950's onwards, few historic buildings remain. Nowadays, Rotterdam's cityscape is determined by post-war reconstruction architecture.

Roost site selection

From the database of the Urban Ecology Research Unit of the Natural History Museum Rotterdam, observations of large groups of swarming pipistrelles, pipistrelles entering a building, or dead young pipistrelles, were used to select potential roost sites. Six known roost sites were visited at daytime to judge suitability for this study. Criteria that were used to select the most suitable sites were the chance on presence of bats (based on observations in preceding years), accessibility to the building and surrounding area, and proximity to other roost sites. Eventually, two roost sites were chosen. Both locations were visited during a morning in April 2018 to ensure bat presence, and were subsequently monitored for a period of 11 weeks, from April 11 to July 4, 2018.

Schiebroek – Berberisweg: One of the roost sites is located in the Schiebroek district in the northern part of Rotterdam (51°57′54″ N, 4°28′24″ E). Pipistrelles have been known to use this roost site for several years. The specific building complex used by bats was built in 1971, mainly functions as a day-care centre for children, and is located at the address Berberisweg 354 (Fig. 1). It is hypothesized that the maternity colony at this roost site alternates between the described location and a school building 500 meters down the road. During several visits, the school

Figure 1 Impression of the Berberisweg building complex in which pipistrelles roost. [T. Voortman]

Figure 2 Impression of the Lakerveld building in which pipistrelles roost. [T. Voortman]

building was checked for activity, but no bats were ever observed there. For this reason, all subsequent visits focused on the day-care centre at the Berberisweg 354. Directly opposite to this building, the Schiebroeksepark is located, a green park covering an area of about 20 hectares.

Zuidwijk – Lakerveld: The other roost site is located in the Zuidwijk district in the southern part of Rotterdam (51°52′14″ N, 4°28′42″ E). The location had been reported as a roost site for pipistrelles before. The particular building in which pipistrelles roost here is a typical post-war flat built between 1945 and 1960 (Kadaster 2018) located at Lakerveld 2-80 (Fig. 2). Adjacent to this flat, four similar flats are situated. The Lakerveld flat is located in between two large green areas with substantial water bodies: the Zuiderpark to the north, and the Pendrechtse Molenplassen to the south.

Monitoring

Bat activity was monitored from April 11 to July 4, 2018. The Berberisweg location was visited nine times, the Lakerveld location was visited eight times (Table 1). Both locations were visited two times in the morning. In the early morning, before returning to their roost site, bats swarm around the roost entrance. Often, individuals make multiple false landings before actually entering the roost (Kunz 1982). At that moment, it is relatively easy to find a bat colony or a specific emergence hole. On all other monitoring days, roost sites were visited during the evening. Pipistrelles then emerge one by one from their roosts, making it easy to count individuals. Roost sites were only monitored when no precipitation or strong wind was predicted (Vleermuisprotocol 2017). Wind speed during monitoring never exceeded 4 Bft. Each observation round started approximately 15 minutes before sunset and ended when bat emergence had stopped for at least 15 minutes (Collins 2016, Vleermuisprotocol 2017). During all visits, the number of emerging bats, as well as onset and end of bat emergence, were recorded.

Monitoring was always performed by two observers using bat detectors. For instant detection and identification of bats via the frequency of echolocation calls, both a Pettersson D240x (Pettersson Elektronic AB) and a Batlogger M (Elekon AG) were used. The latter also functioned as a back-up measure for later reference, as it records all ultrasonic calls while deployed. When monitoring rounds started, observers positioned themselves at corners of the buildings, overseeing at least two walls

Table 1 Overview of bats counted during all visits at the two locations. Numbers with an asterisk (*) indicate visits where location(s) of emergence opening(s) could not (all) be determined. Tilde symbols (~) indicate morning visits where numbers were estimated rather than counted.

	Berberisweg	#bats	Lakerveld	#bats
1st visit	April 11(morning)	not counted	April 18 (morning)	~60
2nd visit	April 11	47	April 19	79
3rd visit	April 23	90*	April 25	113
4th visit	May 3 (morning)	~50	May 8	52
5th visit	May 7	47*	May 28	22*
6th visit	May 17	42*	June 8 (morning)	~60
7th visit	May 31	87*	June 11	130
8th visit	June 12	32*	July 3	125
9th visit	July 4	99		

each (Fig. 3). In this way, all possible emergence openings were overseen at Lakerveld location. At Berberisweg, one observer was positioned at one of the building corners, whereas the other observer was positioned at the central square, overseeing the surrounding walls (Fig. 3A). In this way, chances of missing emerging bats were minimized as much as possible. As soon as multiple bats were seen flying by, observers followed where they came from to track down emergence openings in use. These openings were then observed and times at which pipistrelles emerged were noted. Any other relevant information, like behaviour, flight pattern, the potential presence of predators and weather conditions, was noted as well.

As bats emerge very swiftly from their roost openings and observation conditions are not optimal after sunset when it gets darker every minute, emerging bats may sometimes be missed by the observer and some occupied holes may escape from detection. In order to broaden our view on parts of buildings, both in space and time, camera recordings were made of one or two prior detected emergence holes using a Pulsar Helion thermal imaging scope (XP28), usually at 1.4x magnification and 'rainbow' colour scheme settings. The use of a thermal scope minimized chances of missing emerging bats even further. Recorded videos were viewed on a computer screen the following day to extract information on bat emergence and behaviour. From videos that captured bats emerging from a roost opening, emergence was recorded per second, providing detailed information on the temporal variation in roost emergence. Videos shot with the thermal imaging scope allowed us to slow down and re-watch specific behaviour multiple times, providing a novel way of studying bat emergence behaviour in great detail.

Data analysis

All visual recordings were analysed using Windows Media Player or VLC Media Player. All data was collected in MS Excel. Statistical analysis was performed in R using Pearson's correlation coefficient (R Core Team 2018). No back-up sound analysis was performed with the Batlogger recordings as all bats could already be identified as pipistrelles during monitoring in the field.

RESULTS

Whereabouts of roosts

All bats examined during this study made use of weep bricks to enter and leave their maternity roosts in cavity walls. During most visits, multiple weep bricks were in use as roost opening (Table 2, Table 3). During some visits, no, or not all, positions of roost openings could be found. Total amount of emerging bats (Table 2, Table 3) was defined by the number of bats that were seen emerging from roost openings plus the number of bats that had clearly emerged from the observed building (complex) but could not be traced back to a specific opening.

Pipistrelles make use of many different roost openings during the maternity period: A total of nine different roost openings at three different sub-buildings was identified at the Berberisweg location (Fig. 3A). At the Lakerveld location, ten roost open-

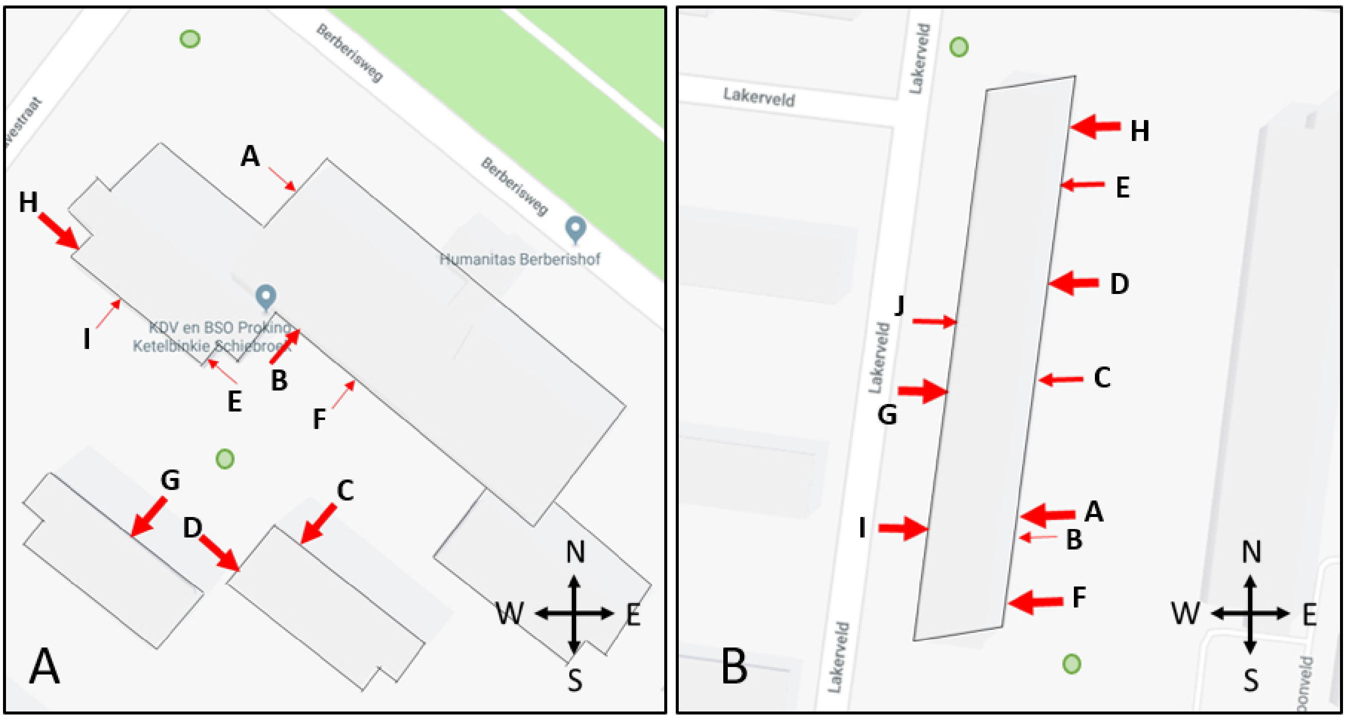

Figure 3 Maps showing building shape (black lines) and positions of occupied roost openings (red arrows) during the monitoring period at **A** Berberisweg and **B** Lakerveld (www.maps.google.com). Identified roost openings were named with one letter in chronological order of discovery (starting from A), numbers of bats per opening and per visit can be found in Table 2 and 3. Thin arrows indicate openings that, during the entire monitoring period, were used by up to 15 individuals, medium arrows indicate openings used by 15-40 individuals, thick arrows indicate openings used by more than 40 individuals in total. Green circles indicate observer start positions at the beginning of each monitoring round.

Table 2 Orientation of walls at which occupied bat roosting sites were found during each visit at the Berberisweg location. The building has walls facing northeast (NE), northwest (NW), southeast (SE) and southwest (SW), each orientation is shown in a column. Numbers represent the amount of bats that emerged from an opening at that wall orientation during the visit specified in the first column. Total number of emerged bats is defined by the number of bats that were seen emerging from specific roost openings plus the number of bats that had clearly emerged from the building complex but could not be traced back to a specific opening. In the last column, one-letter names of openings that were in use during the specified visit are given (see Fig. 3A for names) and number of bats emerging from each opening are indicated between brackets. Numbers with an asterisk (*) represent visits where not all occupied roost openings were found. Tilde symbols (~) indicate morning visits where numbers were estimated rather than counted.

	NE	NW	SE	SW	Total counted	Openings in use
April 11	5	21	2	19	47	B (19), D (13), A (8), C (5), E (2)
April 23	57	15	2		90*	C (57), D (15), E (2)
May 3 (morning)		~50			~50	D (~50)
May 7			7	11	47*	F (9), E (7), B (2)
May 17					42*	
May 31	47				87*	G (47)
June 12					32*	
July 4		87		12	99	H (87), I (12)
TOTAL	109	173	11	42		

ings were identified at the single building that was monitored (Fig. 3B). Both maternity roost locations were visited during the evening every 14 days on average, with intervals ranging from six up to 22 days. During each visit, the majority of bats emerged from different roost openings compared to the preceding visit, indicating that groups switch to a new roost opening often, presumably at least every 10-14 days. During some visits, not all roost openings could be found.

Height: Occupied openings were located at heights ranging from 3 up to about 20 meters (top of building). Buildings were never higher than 20 m. Only a single roost opening was found at a height lower than 6 m, indicating that bats prefer to enter roosts higher up. Generally, openings were at a height of about 10 m.

Wall orientation: Bats emerged from openings in walls facing all directions. At the Berberisweg location, walls occupied by pipistrelles face northwest, northeast, southwest and southeast (Fig. 3A). During most visits, multiple roost openings at different sides of the buildings were occupied (Table 2). Table 2 shows that most bats emerged from walls facing northwest, followed by walls facing northeast. Walls facing southwest and southeast were less preferred.

Table 3 Orientation of walls at which occupied bat roosts were found during each visit at the Lakerveld location. The building is rectangular, with the majority of wall surface facing east (E) and west (W). The limited surface of walls facing north and south provide very few potential roosts, making it unlikely to discover roosts here. Total number of emerging bats is defined by the number of bats that were seen emerging from roost openings plus the number of bats that had clearly emerged from the building but could not be traced back to a specific opening. In the last column, one-letter names of openings that were in use during the specified visit are given (see Fig. 3B for names) and number of bats emerging from each opening are indicated between brackets. Number with an asterisk (*) represent visits where not all occupied roost openings were found. Tilde symbols (~) indicate that displayed numbers were estimated rather than counted.

	E	W	Total counted	Openings in use
April 18 (morning)	~60		~60	A (~60)
April 19	79		79	D (36), A (28), C (13), B (1), E (1)
May 25	113		113	D (87), E (20), C (3), A (2), B (1)
May 8	52		52	F (49), C (2), B (1)
May 28	6		22*	A (2), B (2), C (2)
June 8 (morning)		~60	~60	G (~60)
June 11	130		130	H (117), C (13)
July 3		125	125	I (97), J(28)
TOTAL	440	185		

The building at Lakerveld is a long, rectangular flat with the front side facing west and the back side facing east (Fig. 3B). The limited surface of walls facing north and south greatly lessened the potential of roosts on these walls. During five out of eight visits, bats were only observed at the east (back) side of the flat (Table 3). During two out of eight visits, bats were only observed at the west (front) side of the flat. During one visit, only six emerging bats were observed, providing inadequate information about occupied roost sites during that specific visit.

Heating: Bats roosted in buildings with and without heating. The flat at Lakerveld is inhabited by people and can therefore be regarded constantly heated. Some of the buildings at Berberisweg are used as a day-care or meeting centre during the day. Heating inside these parts of the buildings are on a constant temperature of 21°C (L. Nuijten, BSO Prokino Ketelbinkie Schiebroek, personal communication). Other parts of the Berberisweg buildings are currently out of use and therefore not heated at all. Pipistrelles roosted in both heated and non-heated parts of the Berberisweg building.

Phenology, emergence timing and social behaviour

Emergence timing and behaviour did not differ between the two locations. Therefore, data from both locations were combined in further analyses if not indicated otherwise.

Maternity colonies are already formed in April: At both locations, maternity groups with a high number of individuals were already present from the first visit onwards (Table 1). At the Berberisweg location, 47 pipistrelles were present at the night of April 11, this number increased to 90 bats on April 23. At the Lakerveld location, 79 bats were present at the night of April 19, increasing to 113 bats present on April 25. Group sizes based on all visits are estimated to be around 100 individuals at the Berberisweg location and 130 individuals at the Lakerveld location.

Onset, mean and end of emergence are correlated with sunset: Onset of emergence was significantly correlated with sunset (R^2=0.9677, df=9, p<0.001), as were end of emergence (R^2=0.9393, df=9, p<0.001) and mean moment of emergence (R^2=0.9523, df=9, p<0.001) (Fig. 4).

Optimal moment of emergence: When roost sites were occupied by multiple bats, emergence timing was recorded per minute (n=660). Emergence over time often shows a logistic curve (Fig. 5). Average moment of emergence onset was 17 minutes after sunset, average end was 55 minutes after sunset. Of all bats observed, 95% emerged in the period between 15 and 55 minutes after sunset. 75% emerged between 25 and 50 minutes after sunset. Duration of emergence event ranged from 19 to 44 minutes, mean duration was 35 minutes. Mean moment of emergence was 35.7 minutes after sunset (n=660, Fig. 6).

Bats emerge faster when more individuals occupy one roost opening: Total duration of emergence (time elapsed between moment of first emerging individual and moment of last emerging individual) for a specific roost opening is not correlated to the total number of bats emerging from that roost opening (R^2=0.0152, df=9, p=0.7181), indicating that bats emerge faster from a roost opening when more bats are present inside the roost and waiting to emerge (Fig. 7).

Emergence timing corresponds with wind speed and temperature rather than moment of the year: Mean moment of emergence is not correlated with the moment of the year (number of days after first visit) (R^2=0.098, df=9, p=0.3486), neither is

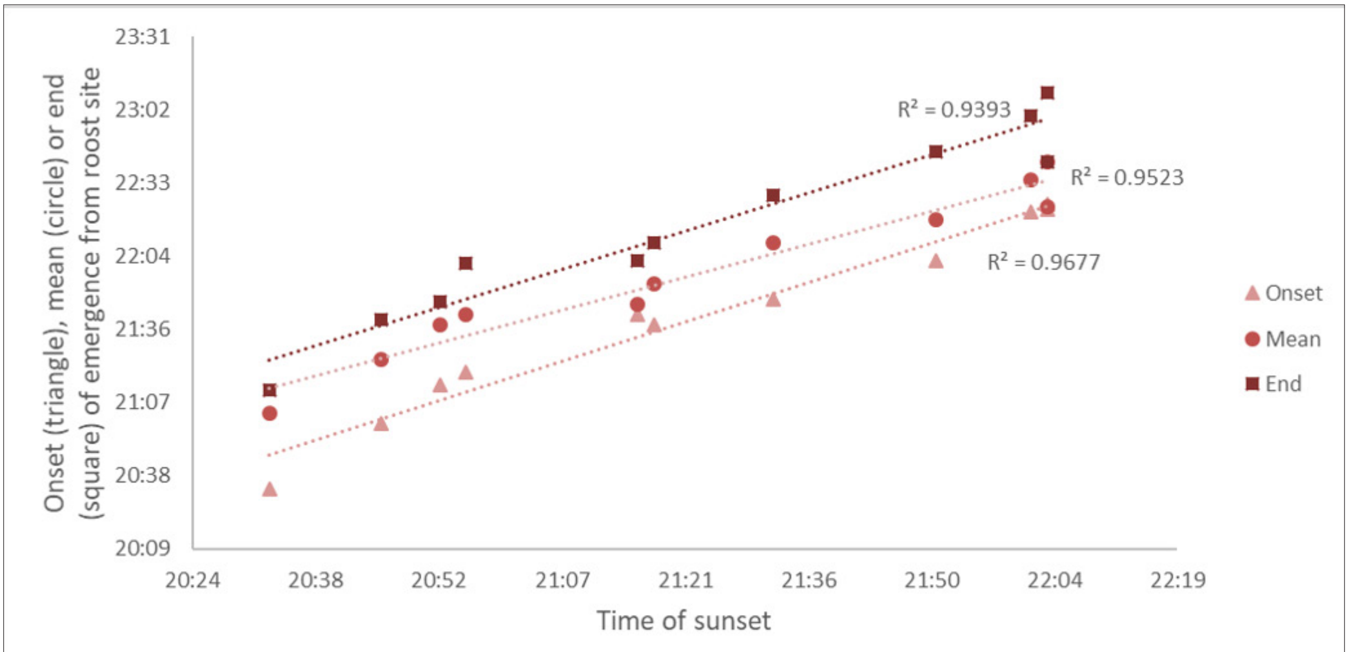

Figure 4 Onset (light red triangle), mean (red circle) and end (dark red square) of emergence are related to sunset (p<0.001). R^2-values are displayed in figure.

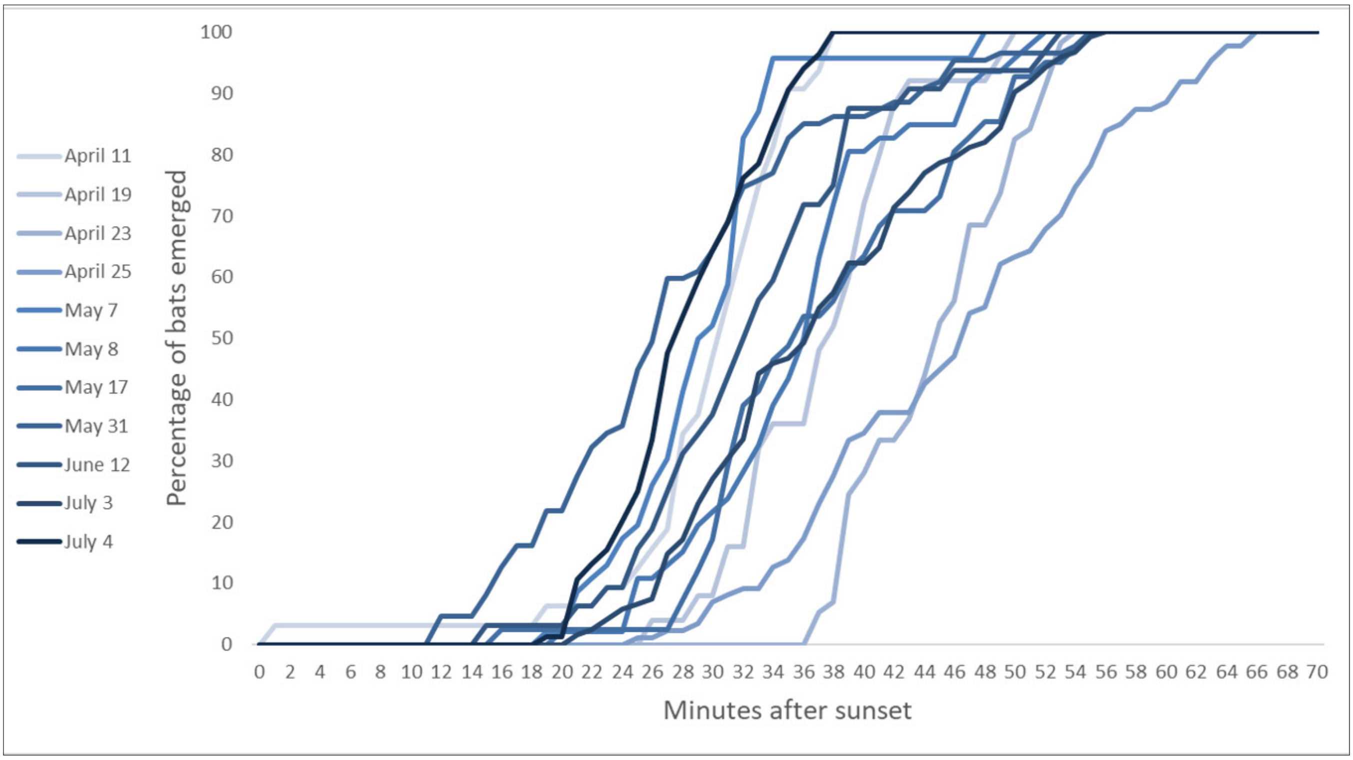

Figure 5 Bat emergence over time in percentages (#of bats counted emerging per minute/#bats counted in total per night*100%).

the total duration of emergence (R^2=0.0282, df=9, p=0.6216). Mean moment of emergence is correlated with wind speed (R^2=0.6878, df=9, p<0.05), being earlier with lower wind speed (Fig. 8 left). Emergence tends to be earlier with higher temperature (R^2=0.3388, df=9, p=0.06; Fig. 8 right). Wind speed tended to be lower with higher temperature (R^2=0.308, df=9, p=0.07637).

Clustering during emergence: Median difference in time between two bats emerging from a single roost site was 11 seconds (n=355). Of all observed bats, 75% emerged from a roost opening within 35 seconds after the previous emerging individual. Only 12% of all bats took more than one minute to emerge after their predecessor. Bats were regularly seen emerging in small clustered groups, where time in between multiple emerging individuals was often only a few seconds (Fig. 9,

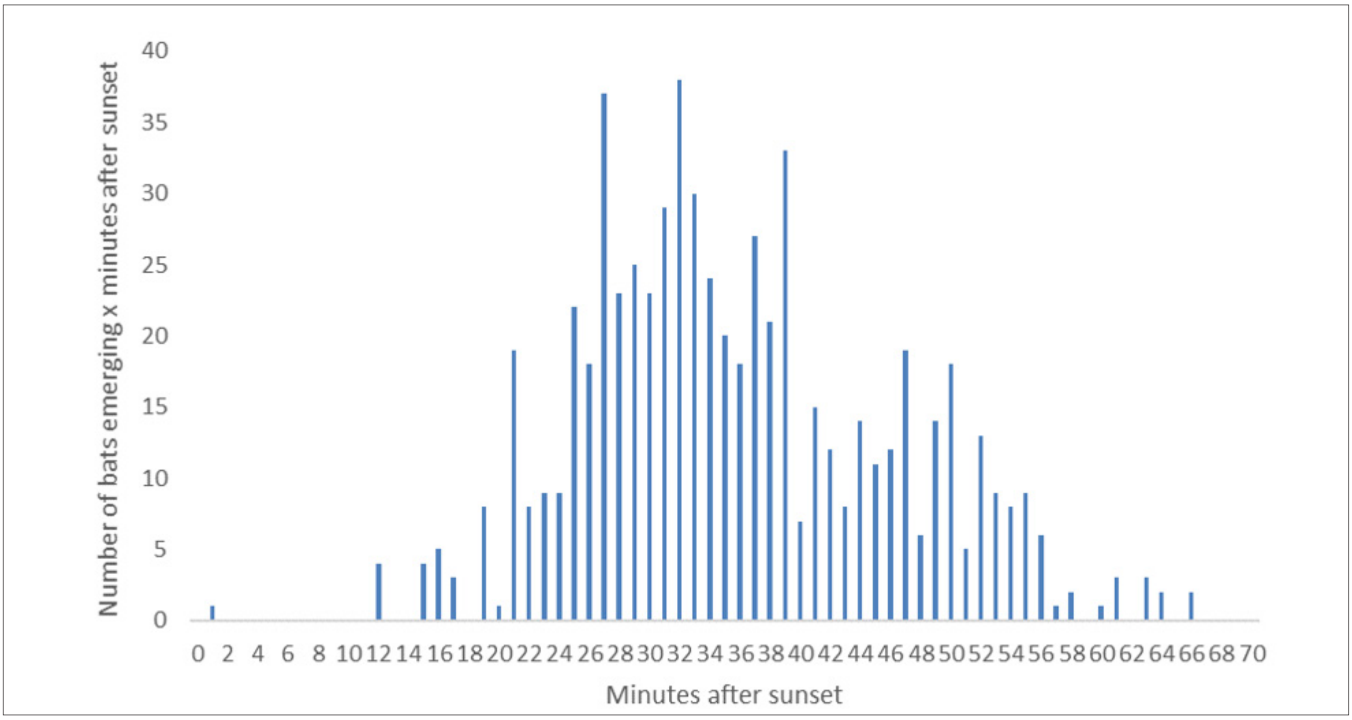

Figure 6 Moment of emergence from maternity roosts is normally distributed. n= 660 emerging bats observed during 11 visits.

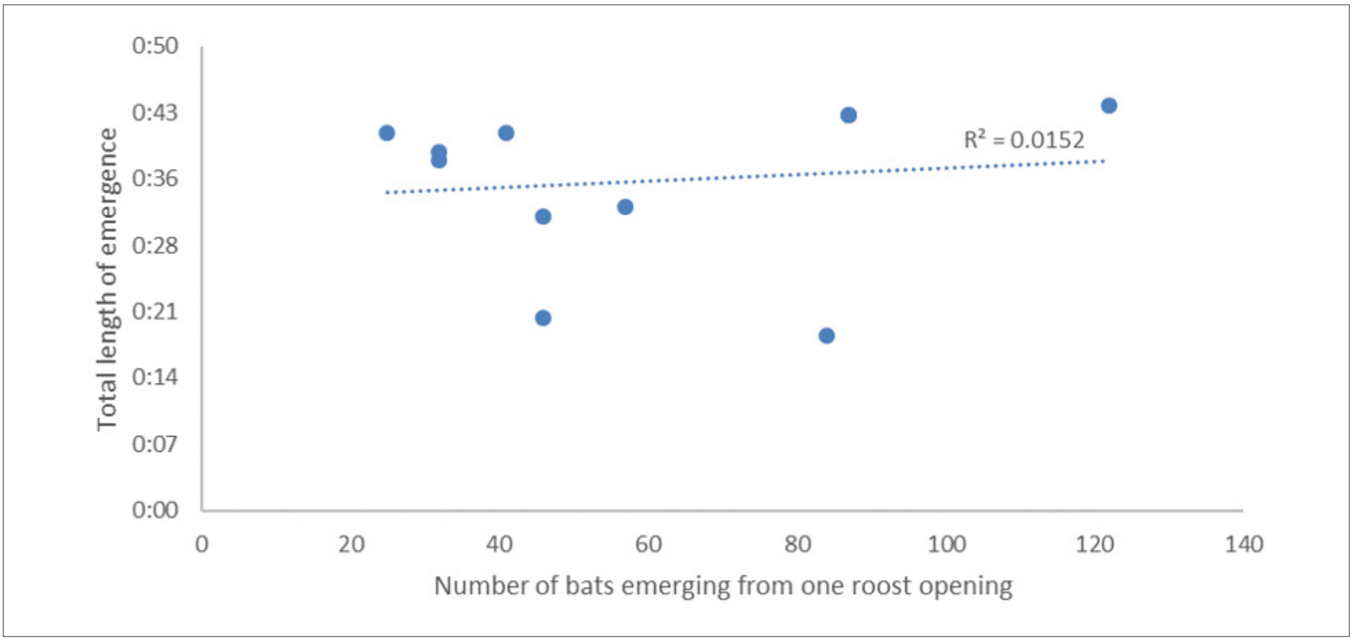

Figure 7 Total emergence duration (last individual – first individual) is not correlated to the number of individuals emerging from one roost opening.

Additional material: Video 1); one-third (32%) of all observed bats emerged within 4 seconds after the previous emerging individual.

Next to clustering together with individuals from the same roost opening, bats were regularly seen emerging when one or several individual(s) from an adjacent roost opening flew past (Additional material: Video 2). The emerging bat then joined passing individuals, moving towards their foraging area together. In some cases, the majority of bats from one roost opening had already emerged while the first bats started emerging from another roost opening.

DISCUSSION

We monitored two maternity colonies of pipistrelles during the summer of 2018 to determine how they behave around and make use of urban roosts during their maternity period, an essential phase of the year. We observed high local dynamics in maternity roosts within a single building (complex), demonstrating that large groups of bats can easily be overlooked when there is insufficient monitoring. Pipistrelles roosted less in south-facing walls compared to walls on other orientations, suggesting that sun-lit walls may be less preferred as roosting site than is often assumed. On both locations, maternity roosts were already established by early April, more than a month before the defined maternity period start date which is currently used as a guideline for taking protective measures. Our data shows that there is an optimal moment of roost emergence for pipistrelle bats at around 36 minutes after sunset, and that this moment might partly be determined by environmental factors like wind speed and temperature. The use of a high resolution thermal camera allowed us to study social behaviour and emergence timing in great detail and unravelled that pipistrelles co-ordinate emergence by forming clusters with individuals from the same or adjacent openings.

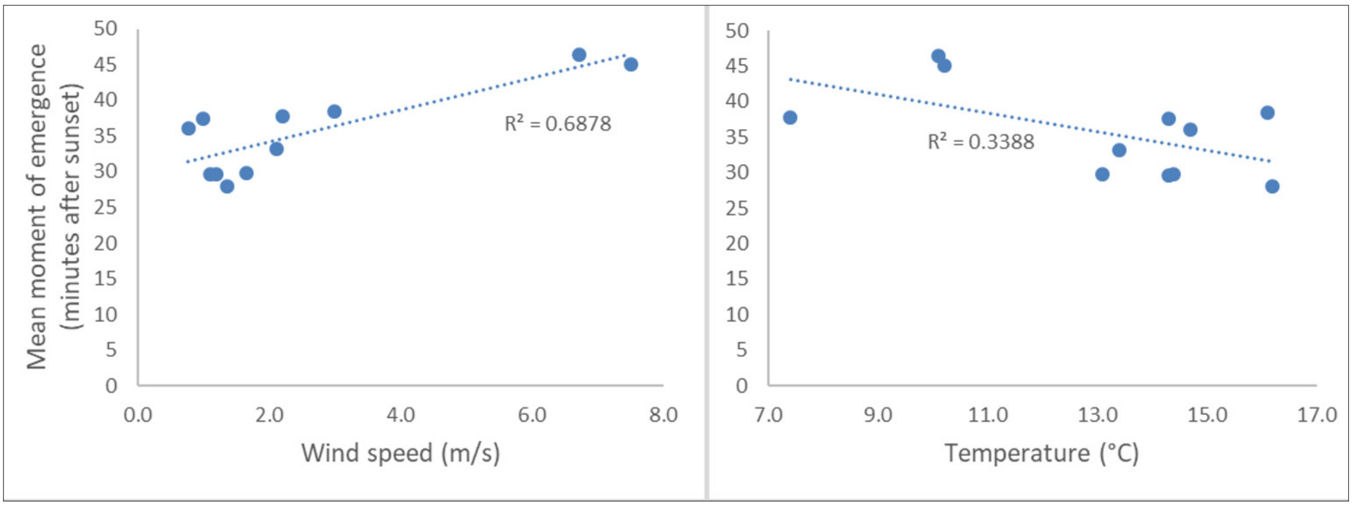

Figure 8 Mean moment of emergence is partly explained by temperature (p=0.06) and wind speed (P<0.05). R^2-values are displayed in the figure.

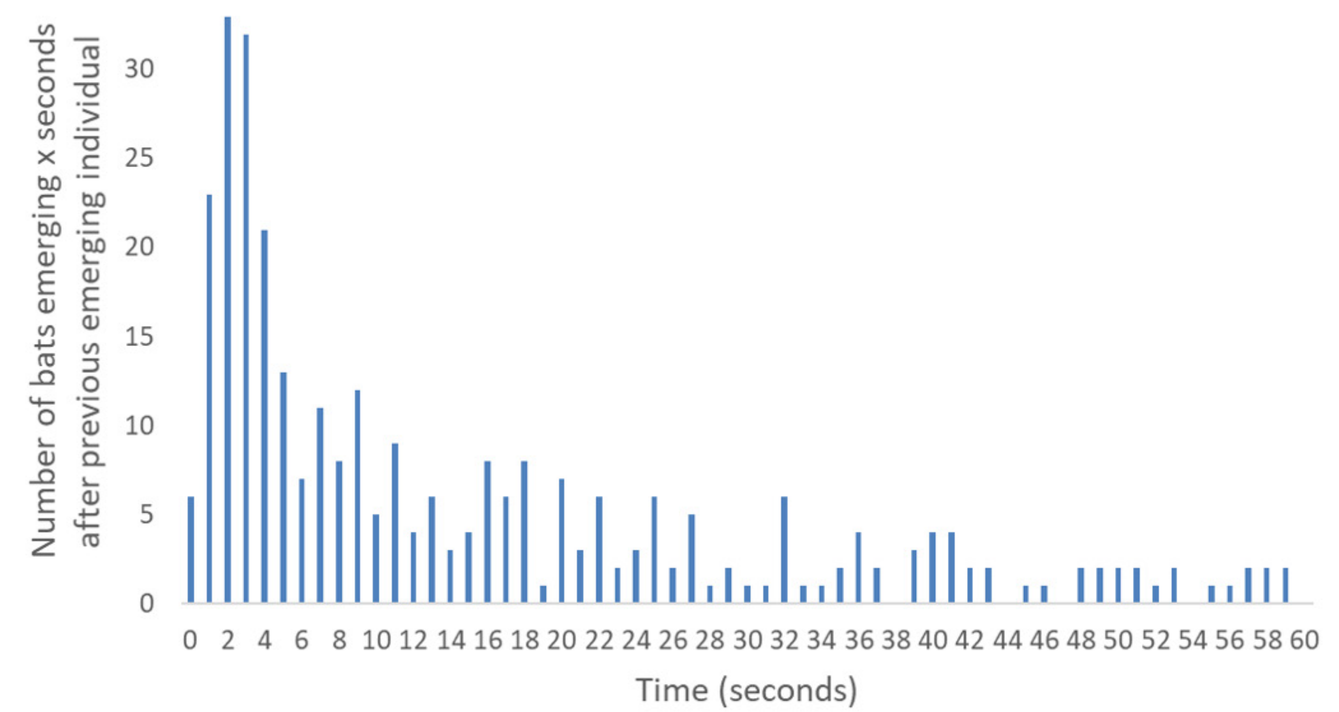

Figure 9 Time (seconds) that last in between two bats emerging from a single opening. Only data for the first 60 seconds after the previous emerging bat is shown (88% of all data). n= 355.

Spatial dynamics: whereabouts of roosts

During the entire study period and on both locations, pipistrelles had moved to another roost opening within the same building (complex) with every visit, indicating that groups switch roost openings frequently, presumably at least every 10-14 days. A similar average duration of roost occupancy was shown by Feyerabend & Simon (2000). Obviously, with a higher monitoring frequency and thus lower visit interval, switching may show to happen even more frequently. The fact that bats switch between roost openings has been known for a long time but often focuses on switching between different buildings that together form a network of roosts. In this study, we show that only a single building or building complex can provide ample space for a network of roost sites that suffice for the entire maternity period. We regularly observed that a part of a building was not in use during multiple monitoring rounds but would suddenly be inhabited by tens or even hundreds of individuals during a next visit. These findings highlight the importance of a thorough study of buildings with (potential for) pipistrelle maternity colonies prior to e.g. construction works. A pipistrelle's flexibility in roost site usage may create the impression that colonies can move to another building whenever the original site is demolished, but their high roost philopatry (Brigham 1991, Thompson 1992, Lewis 1995) emphasizes the importance of conservation of identified occupied roosts. Currently, in The Netherlands, only two monitoring rounds are obligatory to exclude the presence of a maternity roost in a particular (part of a) building before it can be renovated or taken down (Vleermuisprotocol 2017). Our results suggest that more visits are needed before proper conclusions can be drawn on whether (certain parts of) buildings are inhabited by bats. Moreover, it demonstrates that it may be insufficient to spare only a part of a maternity roost building, as the group could be using any other part of the building as well. When taking protective measures, potential roost openings surrounding known roost sites should also be taken into account.

During several visits, only a part of the maternity colony could be rediscovered. Possibly, nearby buildings were sometimes used as alternative roosts. It was previously hypothesized that the Berberisweg group switched to a school building 500 meters to the southeast. During our monitoring rounds, no bats were ever observed there. No alternative roost locations could be found in the close vicinity of the Lakerveld group. Bats are hypothesized to switch roosts to avoid the build-up of parasites (Bartonicka & Ružicková 2013), to maintain social relationships (Willis & Brigham 2004), or to find optimal microclimatic conditions (Callahan *et al.* 1997). As we only monitored the maternity roost locations every two weeks on average, no conclusions could be drawn on the possible relationship between the orientation of walls that bats occupy at a certain moment and the corresponding temperature of that day and night. A more elaborate study with daily monitoring would allow testing whether temperature is a factor that determines at which side of buildings bats choose to spend their days.

Pipistrelles are known to use a wide variety of roost openings, like cracks and crevices, space under crooked roof tiles, and even behind window frames (Kunz 1982, Stone *et al.* 2013). All pipistrelles observed in this study made use of weep bricks to enter their roosts inside cavity walls. Openings were at an elevation of 3 up to 20 meters from ground level. Only one opening was found at 3 m height, all others were at least 6 m up. As the maximum height of the visited buildings was 20 m, no conclusions can be drawn on maximum suitable heights of roost sites.

Pipistrelle bats have been shown to have a very high thermal conductance (Genoud & Christe 2011), emphasizing the importance of an appropriate microclimate in roost sites. Our results demonstrate that during the maternity period, pipistrelles use roost openings on walls facing all directions, contradictory to the general idea that bats prefer roosts on south-facing - hence 'warmer' - walls (see e.g. Soortenstandaard Gewone dwergvleermuis 2014, Bat Conservation Trust UK 2018, Norfolk Wildlife Trust 2018, IOS Wildlife Trust 2013, Wildpro encyclopedia 2018). Overall, at the Berberisweg location where walls facing all directions were available, most pipistrelles roosted on northwest and northeast sides of the building. Walls facing these directions always hosted the majority of bats. Walls facing southwest were occupied several times by multiple individuals but never hosted the majority of the group. Southeast-facing walls were infrequently occupied by only a few bats. At the Lakerveld location, where walls facing east and west were available, bats mostly roosted at the eastern side of the building. However, the entire maternity colony moved to the western side of the building twice, showing that this side was also a suitable roost site. Southern sides of buildings are generally thought to be preferred as roost by bats as they receive most sunlight during the day and thus provide a warmer microclimate than north-facing walls do. Our results show that walls facing south may be less preferred as roosting sites than assumed, whereas walls facing north could be of greater importance, especially during the maternity period when large groups of female bats cluster together to give birth. Given the fact that the temperature in a roost site increases substantially when more bats are present (Roverud & Chappell 1991), sun heated walls facing south could possibly become too warm for bats during the maternity period. This explanation is further supported by the fact that pipistrelles in our study roosted not only in inhabited and thus heated buildings, but also in unoccupied buildings without heating.

These results contribute to our understanding of suitability of buildings as roost sites. In The Netherlands, when known roost sites are disturbed in renovation or demolition practices, laws enforce compensation and mitigation. Preservation of bat-friendly cavity walls or the incorporation of bat boxes in building walls form simple solutions that can solve the apparent conflict between renovation works and bat conservation. Knowledge on the spatial variation in maternity roost site use is essential when planning the installation of such walls and boxes. Our results show that, for maternity roost sites, walls facing north, west and east are at least as suitable as, if not more suitable than, south-facing walls. Both inhabited and uninhabited brick stone buildings can be used to install boxes in, as the presence or absence of heating within a building does not determine its suitability as maternity roost. Together with our finding that bats use all sides of buildings, the high local dynamics within maternity roost buildings emphasizes the importance of availability of multiple roost openings at different orientations. These results are in line with a recently published evaluation of mitigation practices, stating that more openings in a building results in higher chances on occupancy by bats (Lintott & Mathews 2018).

Temporal dynamics: phenology, emergence timing and social behaviour

At both the Berberisweg and Lakerveld location, substantial numbers of bats were already present in monitored buildings by mid-April and more than 80% of the estimated colony members were present by the end of April. These high numbers show that maternity colonies were already established and settled early in the reproductive season. Currently, in The Netherlands, May 15 is recognized as the moment when maternity groups are established and thus vulnerable for construction works (Vleermuisprotocol 2017). Our findings show that maternity colonies can already be present from April onwards, emphasizing that their vulnerability in the weeks preceding May 15 should not be underestimated.

According to weather data collected by the Royal Netherlands Meteorological Institute, the months February and March in 2018 were relatively cold compared to the monthly average in the previous 30 years (1981-2010), whereas the months April and May were relatively warm (KNMI 2020). Higher temperatures in spring may have induced earlier establishment of maternity roost sites. With the current climate change and resulting global warming, higher spring temperatures can be expected in following years too and could eventually lead to a phenological shift in the establishment of maternity roosts. Our results show that maternity roosts may already be established more than a month earlier than currently described, and suggest that the guidelines for taking protective measures should be re-evaluated.

Pipistrelles generally emerged between 15 and 55 minutes after sunset (95% of all bats). Mean moment of emergence was 36 minutes after sunset. In other studies in Europe, comparable mean emergence times were found (Jones & Rydell 1994, Rydell *et al.* 1996, Davidson-Watts & Jones 2006). Moment of emergence furthermore superficially shows a normal distribution, indicating that there is a moment when emergence is optimal, in this case about 36 minutes after sunset. The observation that bats emerge faster when group size is larger supports the conclusion that there is an optimal moment to emerge. Given that bats are low in energy after a day without food, and flight is energetically very costly, being able to determine the optimal foraging moment is essential for an individual's fitness. The optimal moment of emergence can be related to several factors, including avoidance of predators and other aerial-feeding day-active competitors, abundance of prey and hypothermia during daytime (as reviewed in Kunz 1982, Jones & Rydell 1994). Both predation risk and prey insect abundance peak around dusk. Of course, after a full day without food, bats are hungry and thirsty and at a certain moment the risk of getting predated upon will be outweighed by the cost of missing foraging opportunities.

Our results furthermore show that bats emerge earlier with lower wind speed, and tend to emerge earlier with higher temperatures. As wind speed and temperature tended to be (negatively) related, it is impossible to pinpoint which factor plays the most important role for bats in determining their optimal moment of emergence. In fact, both factors could play a role in this decision process. Both high wind speeds and low temperatures are energetically more costly for bats and could thus influence the best moment for arousal (Turbill *et al.* 2008). Furthermore, both factors could indirectly provide bats with information on prey activity. Studies have shown that bat activity around summer roosts coincides with insect activity (Anthony *et al.* 1981). Pipistrelles feed on small insects, often close to water bodies. Activity of some aquatic insects follows a diurnal rhythm linked to light levels (Corbet 1964). Abundance and activity of other nocturnal insects relates to air temperature (Williams 1961). As insects are ectothermic, the temperature of their environment determines body temperature and thus activity. In general, insect activity increases with higher temperatures. For bats, higher temperatures could therefore be an indication of higher prey abundance and could thus be a good cue to emerge earlier.

Davidson-Watts & Jones (2006) found that emergence timing correlates to breeding status, with bats emerging earlier during late pregnancy (June) and lactation (July) compared to early pregnancy (May) and post-lactation (August) periods. Another study shows no effect of reproductive period on emergence timing (Petrželková *et al.* 2006), indicating that this relation remains partly unclear. In our study, maternity groups were only visited a limited number of times during each breeding phase. Also, no information on actual breeding status of present females was available so we could not be sure about the exact phase they were in during our visits. For this reason, no conclusions could be drawn on the effect of breeding status on emergence timing. However, we found no correlation between moment of the year and the mean moment of emergence, showing that emergence timing did not significantly advance or delay during the maternity period.

Overall, our study shows that there is an optimal moment of roost emergence for pipistrelles, and that this moment is probably partly determined by environmental factors like wind speed and temperature. Emergence timing could also be affected by other factors that were not taken into account in this study, for example environmental factors like the amount of lighting and tree cover (Jenkins *et al.* 1998).

Bats were frequently seen emerging from roosts in clusters of multiple individuals rather than alone. There are several explanations for this clustering behaviour, with the most logical ones being 1) anti-predation behaviour, and 2) co-ordination of foraging behaviour. The first explanation is based on the selfish herd theory, as described by Hamilton (1971), which encompasses that individuals within a population can reduce risk of getting caught by predators by being surrounded by conspecifics. If more bats emerge at the same time, they are higher in numbers, thereby decreasing predation risk per individual. The second explanation involves collaboration: bats emerging together and consequently moving to their foraging area in a cluster may be more efficient in examining potential foraging sites and exploiting patches of prey (Wilkinson 1992). The idea that bats communicate to co-ordinate emerging and foraging, is supported by the frequent observation of bats returning to the roost openings a few minutes after emergence had started. These individuals would never re-enter the roost site, but would fly around the opening while producing calls and sometimes make false landings. Such false landings have been described before (Kunz 1982) and were also very frequently observed during morning visits, when the majority of individuals made multiple false landings before entering a roost opening. This behaviour has been studied in several other bat species and is hypothesized to either provide conspecifics with information on roost location or to contact individuals that are inside the roost (Voûte *et al.* 1974, Vaughan & O'Shea 1976, Wilkinson 1992, Kunz & Anthony 1996).

Apart from clustering with individuals from the same roost opening, bats were regularly observed emerging from roost openings when an individual from an adjacent opening flew past. This so-called co-clustering behaviour, as described by Speakman *et al.* (1995), may have the same causes as the general clustering behaviour. Moreover, it suggests that individuals communicate not only within one roost opening, but also with individuals in adjacent roost openings to co-ordinate emergence timing.

Sometimes, onset of emergence from one opening was later than the end of emergence from an adjacent opening. This pattern could be coincidental, but it could also be that bats from different openings emerge at different time windows on purpose as another way of reducing predation risk. Thus, this behaviour might also be the result of communication between bats in different openings to co-ordinate emergence timing. Further research is needed to test these hypotheses.

CONCLUSIONS

This study aimed to describe how pipistrelles make use of maternity roosts in urban environments. Knowledge on pipistrelle behaviour at roost sites is valuable in the process of taking protective measures prior to renovation and demolition works, and is therefore essential for pipistrelle conservation.

We show that only a single building (complex) can provide plentiful space for an entire maternity colony throughout the maternity period, demonstrating that single buildings can be of utmost importance for a colony. Our finding that pipistrelles frequently switch to new roost openings illustrates that groups can easily be overlooked during monitoring, and emphasizes the importance of sufficient research on potential maternity roost buildings before construction works start. Currently, only two monitoring rounds are obligatory to exclude the presence of a maternity roost in a particular (part of a) building before it can be renovated or taken down (Vleermuisprotocol 2017). Our results show that more visits are necessary before proper conclusions can be drawn on whether (certain parts of) buildings are inhabited by bats. Furthermore, we show that maternity colonies can already be established by early April, whereas currently May 15 is defined as the start of the maternity period (Vleermuisprotocol 2017). These findings suggest that guidelines for taking protective measures should be reconsidered.

During evenings, pipistrelles often emerged from their roosts in clusters with individuals from the same or adjacent openings. The use of a high resolution thermal camera allowed us to study this social behaviour and emergence timing in great detail and is recommended for similar studies in the future. We describe that there is an optimal moment of roost emergence at 36 minutes after sunset, and that this moment might partly depend on environmental factors like wind speed and temperature outside the roost. Our results show that maternity groups can establish in both heated and non-heated buildings. Also, we show that pipistrelles roosted less in walls facing south compared to other orientations. These findings challenge the often-assumed preference for sun-lit and indoor-heated buildings, and provide useful insights for conservation planning.

In conclusion, by describing spatial and temporal dynamics in pipistrelle maternity roosts in an urban environment, our results contribute to knowledge on pipistrelle conservation which is needed to safeguard their persistence in anthropogenic landscapes.

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ADDITIONAL MATERIAL

Video 1 Clustering behaviour: pipistrelles emerging in clusters during two different sampling evenings at Lakerveld (April-July 2018). From 00.00-00.48, a first cluster consisting of four individuals emerge from 00.12-00.19, followed by a second cluster with two individuals (00.36-00.38). From 00.49-01.39, a first cluster of three individuals emerge from 01.04-01.12, followed by a second cluster of five individuals from 01.28-01.37. Video available at: https://www.hetnatuurhistorisch.nl/fileadmin/user_upload/documents-nmr/Publicaties/Deinsea/Deinsea_19/Voortman_Bakker_2020_Video1.mp4 [T. Voortman]

Video 2 Co-clustering behaviour: pipistrelles showing co-clustering behaviour. The first half of the video shows three different moments (around 00.05, 00.14 and 00.23) where individuals emerge when another individual flies past at the Lakerveld building (April-July 2018). At 00.23, the bat that shows co-clustering behaviour emerges in the top left corner of the video. The second half of the video shows co-clustering behaviour at the Berberisweg building (April-July 2018). Around 00.34 and 00.44, bats emerge from an opening in the top right corner of the building after a cluster of bats emerged from an opening around the corner (top left) and then flew past. Video available at: https://www.hetnatuurhistorisch.nl/fileadmin/user_upload/documents-nmr/Publicaties/Deinsea/Deinsea_19/Voortman_Bakker_2020_Video2.mp4 [T. Voortman]

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