Effects on hibernating bats of ambient temperatures and the characteristics of winter roosts in a dune area

Annemieke van Zuijlen & Dick Groenendijk

PWN, Zeeweg 12, NL-2051 EC Overveen, the Netherlands, e-mail: annemieke.van.zuijlen@pwn.nl

Abstract: The Dutch dune areas between Zandvoort and Bergen aan Zee contain various sites, such as bunkers and ice cellars, in which bats hibernate. The bats in these sites are counted annually each winter. This study investigates whether the ambient temperatures and other characteristics of these winter roosts influence the number of bats hibernating in them. The relationship between the number of bats counted (average number per location) and the ambient temperatures appears to depend on the species. This relation was absent in Daubenton's bats (*Myotis daubentonii*). The more cold-tolerant brown long-eared bat (*Plecotus auritus*) and Natterer's bat (*M. nattereri*) showed a negative relationship with the ambient temperatures: the warmer it was, the fewer bats of these species were observed in the studied locations. This also applies to the pond bat (*M. dasycneme*), which is known to be less cold-tolerant. The number of bats counted in the winter roosts seems to be mainly related to the size of the sites: the larger the volume of the hibernaculum, the more bats were found there. The humidity, susceptibility to disturbance, the number of rooms and the hiding opportunities in the winter roosts also had an effect on the number of bats. However, the effects of these characteristics were less pronounced than the influence of the size of the sites and differences were not always significant. This knowledge is important in determining guidelines for management and to be able to evaluate the censuses. This approach, can help ensure that there are enough sites available to provide suitable hibernacula.

Keywords: winter roosts, outdoor temperatures, dimensions, humidity, susceptibility to disturbance, hiding possibilities, pond bat, Daubenton's bat, brown long-eared bat, Natterer's bat.

Introduction

In Zuid-Kennemerland National Park (Nationaal Park Zuid-Kennemerland; NPZK) and the Noordhollands Duinreservaat (NHD) there are many bunkers and other structures, such as ice cellars, in which bats hibernate. To maintain a sustainable population of bats, it is important that all the habitats they require are in a suitable condition. Winter roosts are an important part in this network. Hibernating bats are counted annually within the framework of the national programme, 'the Ecological Monitoring Network' (NEM). These annual censuses are carried out within a fixed period between mid-December and mid-February on the assumption that this is when the maximum number of bats are present in the hibernacula. It is important to know whether or not this is actually true. Therefore, in this study, we look at the relationship between the number of bats in the winter roosts and the ambient temperatures. In addition, there is a need for clear guidelines for managing hibernation roosts. We know which sites are attractive, but less is known about the properties that determine the success of these winter roosts. Such information can allow us to make direct investments in adapting the sites that have the highest potential as winter roosts.

Research shows that the number of animals in a roost can vary greatly during the course of a winter. This is partly because some individuals, especially of cold-tolerant species such as Natterer's bat (*Myotis nattereri*) and brown long-eared bat (*Plecotus auritus*), do not arrive until it gets too cold for them outside, when other winter roosts, such as tree holes and poorly insulated spaces in buildings, become unsuitable. Pond bats (*M. dasycneme*) and Daubenton's bats (*M. daubentonii*) are known to occupy winter roosts relatively early in the year, although it is not known whether this is related to ambient temperatures, insect supply or an early mating season in these species (Haarsma 2013).

Weather conditions during the winter census therefore can influence the bats' choice of specific winter roosts and the numbers present in each. This can cause the numbers to be underestimated in warm weather conditions because not all the animals are in the winter roosts. When determining trends, it is assumed that the maximum numbers of bats are present in the hibernating roosts on the date of the census. To assess the accuracy of counts, it is important to know the influence of the outside temperatures on the number of counted bats.

The most important factors that determine the suitability of winter roosts for bats are: temperature, humidity, human disturbance and darkness (Limpens et al. 1999, Haarsma 2018). Temperatures in the hibernacula should not drop below freezing point and should not fluctuate much, and there should not be too much light. The size of the hibernaculum, the number of rooms, entrances and other openings can influence these characteristics. Humidity must be high and the walls sufficiently rough for bats to be able to hold on. The importance of these properties in winter roosts differs between species (Siivonen & Wermundsen 2008). Some species prefer to hide in crevices, cracks and other holes in the walls, while other species hang free and exposed on the walls. This means that there should be sufficient suitable opportunities for bats to hide and hang and the dimensions, number of rooms and the internal design of the roosts are important for these aspects. Disturbance is unfavourable as it causes the air to move and the temperature in the roost could rise. This may wake up the bats from torpor, causing them to lose extra energy, and lowering their chances of surviving the winter period and reproducing in spring (Haarsma & de Hullu 2012). Disturbance is diminished by a remote and sheltered location or the physical closure of the site. Finally, the bats must also be able to easily find and approach the winter roosts. The location in the terrain, the orientation and shelter of the entrance and the location in relation to other sites (i.e. in a cluster or alone) can influence this.

Although it is known which sites are more attractive as winter roosts, little research has been done into why one roost does better than another. It seems that large, damp sites (with very high humidity and/or water on the bottom and/or the walls and ceilings) are the most successful, but relatively large numbers of bats are also regularly found in smaller and/or drier roosts. Currently, winter roosts are often managed without any substantiated information. Research of the influence of these traits on the number of hibernating bats is therefore valuable for the management of winter roosts.

Material and methods

This study covered 116 hibernacula located within the NPZK and the NHD. Of these, 71 are in the NPZK and 45 in the NHD (figure 1). Among many others, these are the sites where bat numbers are counted annually. The majority are bunkers, but there are also some ice cellars, a water cellar and a gatehouse. Data from the NEM from 1990 onwards, where available, were used for each hibernac-

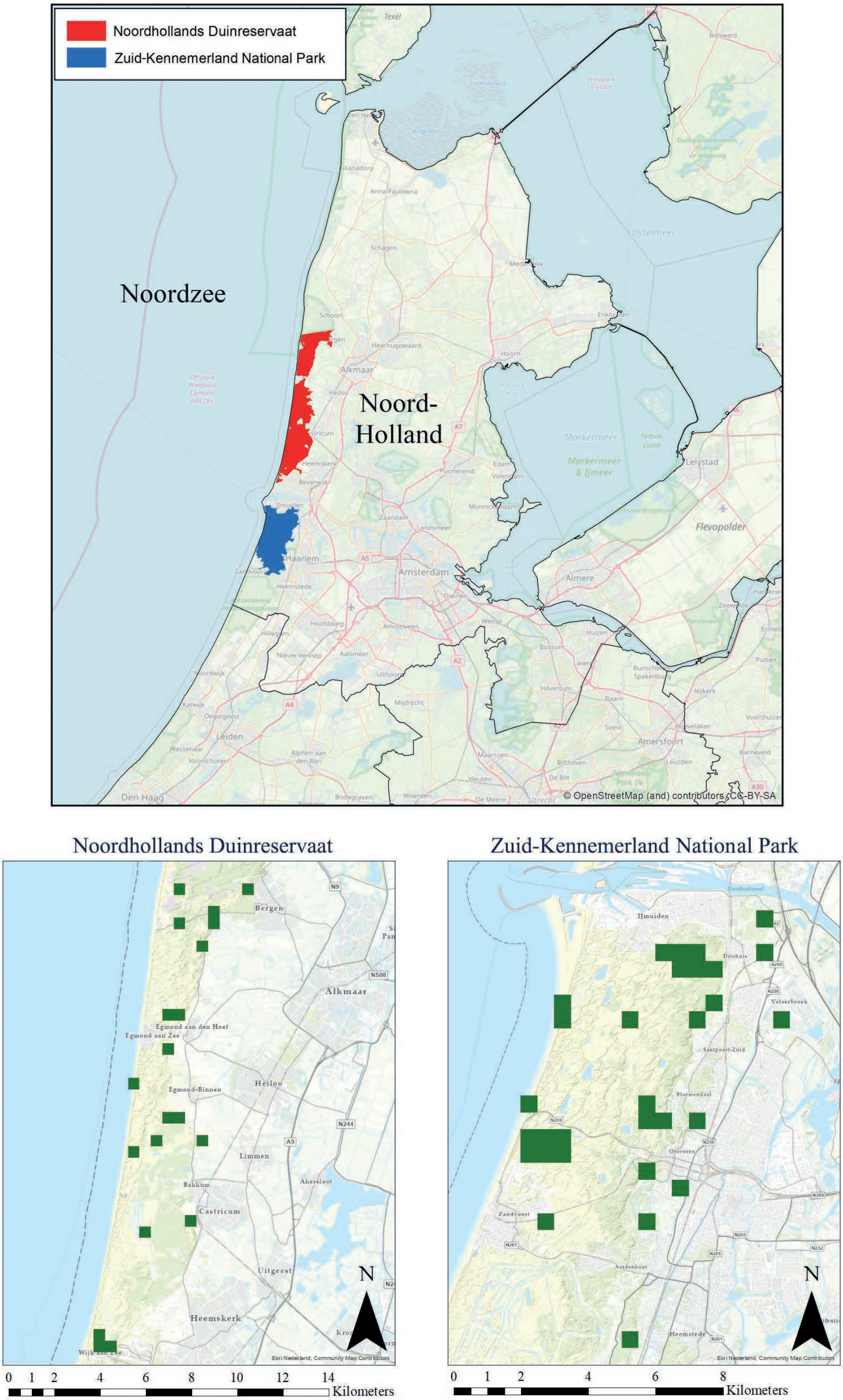

Figure 1. Location of the Zuid-Kennemerland National Park and the Noordhollands Duinreservaat. Below: 500x500 metre squares in which the winter enclosures were located in both areas.

Table 1. Overview of the properties examined, the corresponding categories and their classifications.

Characteristic	Category	Division
Dimensions	Small	0-35 m^3
	Medium	36-150 m^3
	Large	151-400 m^3
Landscape zone	Zeeduin	Location as defined in Natura 2000 Management Plans (Provincie Noord-Holland 2017a, 2017b)
	Middenduin	
	Binnenduin	
Sensitivity to disturbance	Very sensitive to disturbance	Not locked and easy to find
	Fairly / Moderately sensitive to disturbance	Closed but easy to find or not closed and relatively difficult to find
	Not sensitive to disturbance	Closed and not easy to find or not closed and very difficult to find.
Shelter entrance	Sheltered	Entrance partly or completely shielded from surroundings by vegetation
	Exposed	No vegetation in front of entrance
Humidity	Wet	Water on the bottom, walls and ceilings
	Humid	Water on the walls and ceilings, bottom dry
	Dry	Dry bottom, walls and ceilings
Climate stability	Stable	Little draft, only one opening
	Moderately stable	Moderate draft, several openings
	Not stable	Many drafts, many openings
Hiding possibilities	None	As documented in the Portal of the Mammal Society
	Cracks, crevices and clefts	
	Holes	
	Ventilation pipes	
	Behind boards/bricks/stones	
	Combinations of the above	
Number of rooms	1 room	
	2 rooms	
	3 or more rooms	
Orientation of entrance	N	Orientation of entrance
	NE	
	E	
	SE	
	S	
	SW	
	W	
	NW	
Location in a cluster	Not applicable	Mean distance to the four nearest sites.

ulum. To determine the relationship between the number of bats and the outside temperatures, the average daily temperature over the five days prior to the census was calculated, based on the recorded weather data (KNMI, undated) from the nearest KNMI weather stations at IJmuiden and Wijk aan Zee, if available. If data were not available from either station, data from the Schiphol weather station were used. The relationship between these temperatures and the average number of bats per location and per counting date was studied and the relationships were established for the following species: Daubenton's bat, pond bat, Natterer's bat and brown long-eared bat. Dates on which bats were recorded in less than four sites were omitted.

The internal characteristics of as many sites as possible (divided into a number of categories) were detailed (table 1). Some of these categories were based on the Mammal Society's portal (climate stability, hiding possibilities) and others were determined by available local knowledge. Due to the Covid-19 pandemic, the 2021 winter census did not take place and not all the characteristics of the sites were recorded *in situ*. The data gap was filled with information available from the portal of the Mammal Society, supplemented with the knowledge of counters and managers. Where information was lacking for particular variables these were omitted from the analysis. The number of bats per site was taken from the average recorded number of hibernating bats in the 2016-2020 annual censuses.

Statistical analysis

The relationship between the number of bats and the ambient temperatures was determined using simple linear regression. The influence of the different properties of the inhabited sites on the number of bats found was determined using a Kruskal-Wallis test. Subsequently, a post hoc test, the Dwass-Steel-Critchlow-Fligner pairwise comparison (The Jamovi Project 2020), was conducted to determine significant differences between categories. Jamovi, SPSS and Excel were used for the statistical analyses.

The relative influence of the properties studied was determined using multiple linear regression. The scored variables were combined to determine their relative influence on the number of bats counted. Only the statistically significant variables were included in the model. In advance, the multicollinearity was investigated to determine whether any properties in the regression analysis were too strongly correlated with each other to be included in the analysis. Further explorations were carried out, in which the models were built in several different ways (de Vocht 2012) but this did not show any deviating abnormal results.

Results

Influence of external temperatures on the number of bats counted

In both the NPZK and the NHD, no relationships were found between the number of Daubenton's bats and the outside temperature (Linear regression NPZK: $F(1,27)=1.15$, $P=0.29$; NHD: $F(1,34)=1.4$, $P=0.25$). However, there was a clear negative relationship between the number of brown long-eared bats and the outside temperature. The higher the average daily temperature measured over the five days prior to the count, the fewer hibernating brown long-eared bats were found (NPZK: $F(1,27)=4.6$, $P<0.05$; NHD: $F(1,34)=6.7$, $P<0.05$). The same relationship was found for Natterer's bat ($F(1,27)=7.5$, $P<0.05$) and pond bat ($F(1,27)=9.3$, $P<0.01$) in the NPZK (figure 2 and figure 3). There were insufficient observations of these two species in the NHD to analyse.

The influence of the sites' properties

The analysis of variance on the different properties of the sites showed that a large size ($\chi2(3)=12.5$, $P<0.01$) and a large number of different spaces ($\chi2(2)=7.1$, $P<0.05$) had a positive effect on the number of hibernating bats. High humidity ($\chi2(2)=6.9$, $P<0.05$) also seemed to contribute, given the almost significant relationship (post hoc, wet-dry: $P=0.06$). A high susceptibility to disturbance ($\chi2(2)=20.9$, $P<0.001$) and the absence of hiding possibilities ($\chi2(7)=15.3$, $P<0.05$) had a negative effect on the number of hibernat-

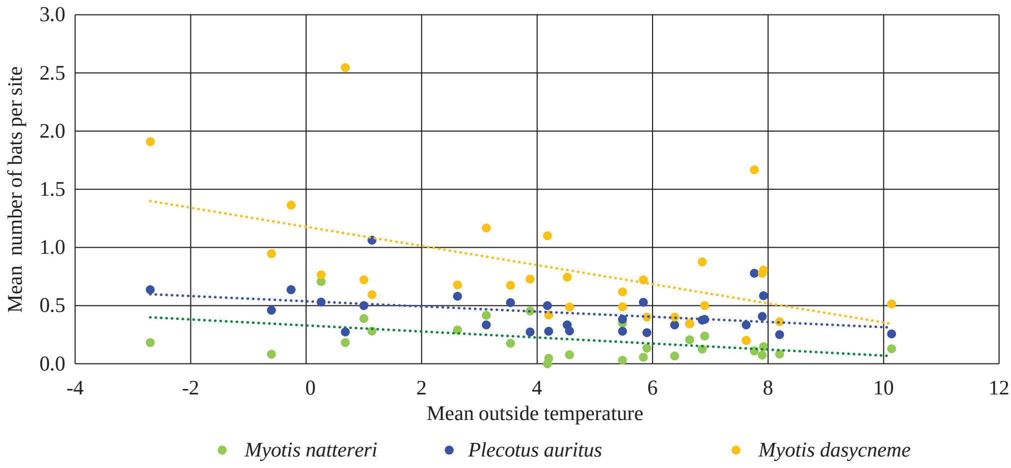

Figure 2. The relationship between the outside temperature and the average number of bats per site in the Zuid-Kennemerland National Park.

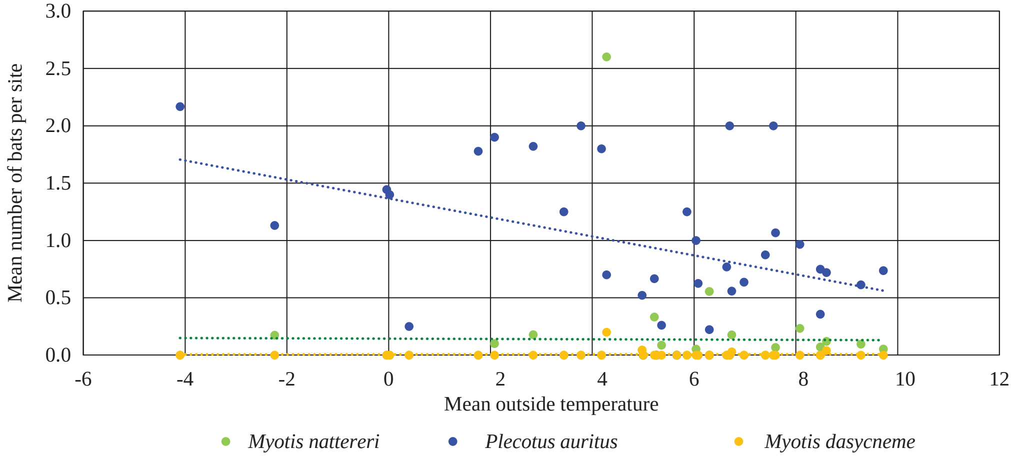

Figure 3. The relationship between the outside temperatures and the average number of bats per site in the Noord-hollands Duinreservaat.

ing bats (figure 4). The multiple linear regression resulted in a statistically significant model ($F(3,30)=19.4$, $R^2=0.66$, $P<0.001$). The model shows that 66% of the variance in the number of bats counted can be traced back to the categories 'large', 'dry' and 'cracks/crevices', with size having the greatest effect ('large': $\beta=26.6$, $P<0.001$; 'dry': $\beta=-5.6$, $P<0.05$; 'cracks/crevices': $\beta=8.5$, $P<0.05$). The location in the terrain, shelter, location in a cluster and orientation of the entrance had no demonstrable influence on the number of bats, or there were insufficient data to demonstrate a relationship.

Discussion

Temperatures

Several studies have demonstrated or suggested a link between ambient temperatures and numbers of hibernating bats

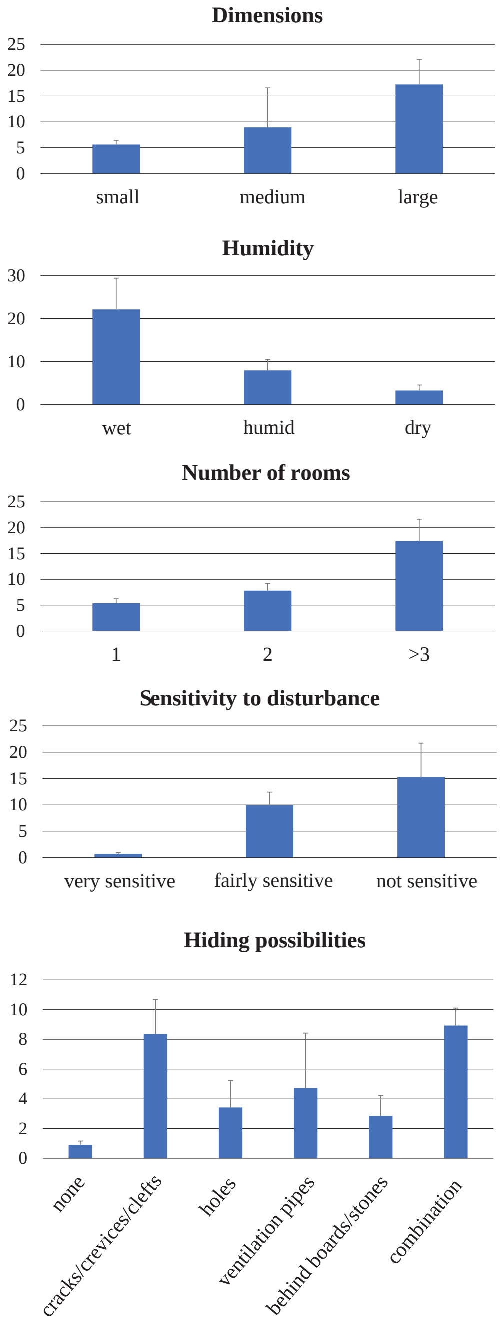

Figure 4. The influence of characteristics with a significant influence on the average number of bats counted per site in the years 2016-2020. Error bars display standard errors.

(Haarsma 2013; see also the contributions of Bekker and Verhees et al. 2022, in this issue). Bats may benefit from the persistent low winter temperatures in climatic zones with severe winters as they are in a deeper state of torpor, wake up less easily and therefore lose less energy (Haarsma & Kaal 2016). This study found a relationship between the outside temperatures and the numbers of counted specimens for some species of bats, although not Daubenton's bats. However, there was a negative relationship between the outside temperature and the number of hibernating brown long-eared bats and Natterer's bats, which are both more tolerant of the cold. The higher the temperature, the fewer bats of these species were found hibernating in these sites. It may be that during relatively warm winters these cold-tolerant species choose other, less temperature-buffered, hibernacula like hollow trees and buildings. Pond bats show the same relation: while they are not known to be pronouncedly cold-tolerant they are, nonetheless, often found in relatively cold places within bunker complexes (Batweter 2021). An increase in winter temperature, due to climate change, could in the future lead to a decrease in numbers of hibernating pond bats, brown long-eared bats and Natterer's bats in winter roosts where bats are counted.

The size, complexity and humidity of hibernacula

This analysis showed that larger hibernating roosts, with more complex sites, contained more hibernating bats. This suggests that a lack of hiding opportunities negatively affects the numbers of hibernating bats. High humidity also contributed greatly to the number of hibernating bats. Other studies have found the size of a winter roost, combined with the number and diversity of hiding opportunities, to be important in bats' choice of winter accommodation (Haarsma 2011, de Boer et al. 2013). A positive relationship between the size of the cave and the population size and species richness has also been demonstrated in caves. Both number of bats and species also appeared to be related to the diversity in hiding opportunities (Furey & Racey 2016). Although humidity in winter roosts has not been considered a crucial factor in previous studies (Haarsma 2011, de Boer et al. 2013), moisture is important for hibernating bats. Bats sometimes have to interrupt their hibernation to replenish moisture loss (Ben-Hamo et al. 2013). These arousals cost a lot of energy, so it is important to limit these.

Sensitivity to disturbance

This research has shown that fewer bats hibernate in winter roosts with a high risk of disturbance. Perhaps bats anticipate disturbance by not choosing these sites as winter roosts, or perhaps they move to quieter places if disturbed. It is not known whether any disturbances actually took place in these disturbance-sensitive sites.

Multiple studies show that disturbance of bats during hibernation has a negative effect on their chances of surviving the winter (Speakman et al. 1991, Thomas 1995, Haarsma 2011, Furey & Racey 2016). Hibernating bats respond to non-tactile stimuli such as light, sound, temperature differences, air flow as well as to tactile stimulation. Bats often awaken after a (non-tactile) disturbance caused by a human visit and may subsequently wake up other bats. As a result, the disturbance can last much longer than the actual visit. Upon awaking, bats burn extra fat reserves, which can damage the chance of female bats bearing young in the spring. Young animals with a relatively small fat supply are most at risk of death.

Conclusions

This study shows the aspects that are important for bats when choosing suitable winter roosts. In particular, the size and the presence of sufficient hiding opportunities are important. High humidity also seems to have a positive effect. For a site manager, it may be important to secure sites so as to minimize disturbance, if necessary, by closing them off to unwanted visitors. These findings may help improve the suitability of sites as winter roosts for bats, that are able to harbour healthy bat populations. In addition, the correlation found between bats and ambient temperatures can be used to critically assess trends among certain species and to determine the optimal census period.

Acknowledgements: You never perform a study on your own, therefore we want to thank all the bat experts who helped us set up this research, especially our colleagues from PWN, Natuurmonumenten and Staatsbosbeheer for their input about winter roosts. We also thank all the counters who have been selflessly committed to the protection of bats for years and, especially, Jan Boshamer, who has coordinated these counts for years and ensured that the counts are as accurate as possible. We also thank the Dutch Mammal Society for collecting and sharing this information. Without all of you, this research would not have been possible. Thanks also to Nick Parrott for his valuable suggestions to improve the English of the manuscript.

References

Batweter 2021. Pond bat informatie. https://www.batweter.nl/index.php/literatuur-en-data/pond bat-informatie.

Bekker, J.P. 2022. The relationship between the numbers of hibernating brown long-eared bats (*Plecotus auritus*) and weather conditions (ambient temperatures and precipitation). Lutra 65 (1): 189-199.

Ben-Hamo, M., A. Muñoz-Garcia, J.B. Williams, C. Korine & B. Pinshow 2013. Waking to drink: rates of evaporative water loss determine arousal frequency in hibernating bats. Journal of Experimental Biology 2016 (4): 573-577. https://doi.org/10.1242/jeb.078790

de Boer, W.F., S. van de Koppel, H.J. de Knegt & J. Dekker 2013. Hibernation site requirements of bats in man-made hibernacula. Ecological Applications 23 (2): 502-514. https://doi.org/10.1890/1051-0761-23.2.502

de Vocht, A. 2012. Basishandboek SPSS 20. Bijleveld Press, Utrecht, the Netherlands.

Furey, N. & P. Racey 2016. Conservation ecology of cave bats. In: C. Voigt & T. Kingston (eds). Bats in the Anthropocene: Conservation of bats in a changing world: 463-500. Springer, Cham, Switzerland. https://doi.org/10.1007/978-3-319-25220-9_15

Haarsma, A.-J. 2011. Hollandse meervleermuizen in winterslaap. Holland's Duinen (58): 3-6.

Haarsma, A.-J. 2013. Het verloop van het aantal vleermuizen in een winterverblijf. VLEN Nieuwsbrief 70. https://www.batweter.nl/attachments/article/4/2013_Haarsma_Het%20verlooop%20van%20het%20aantal%20vleermuizen%20in%20een%20winterverblijf.pdf

Haarsma, A.-J. 2018. Vleermuizen en ecologische verbindingen. Tussen Duin en Dijk 17 (3): 38-41.

Haarsma, A.-J. & E. de Hullu 2012. Keeping bats cool in the winter: hibernating bats and their exposure to 'hot' incandescent lamplight. Wildlife Biology 18 (1): 14-23. https://doi.org/10.2981/10-067

Haarsma, A.-J. & R. Kaal 2016. Predation of wood mice (*Apodemus sylvaticus*) on hibernating bats. Population Ecology 58: 567-576. https://doi.org/10.1007/s10144-016-0557-y

KNMI (z.d.). Daggegevens van het weer in Nederland. https://www.knmi.nl/Nederland-nu/klimatologie/daggegevens

Limpens, H.J., P.H. Lina & A.M. Hutson 1999. Action plan for the conservation of the pond bat (*M. dasycneme*) in Europe. Nature and Environment 108. Council of Europe, Strasbourg, France. https://doi.org/10.13140/RG.2.2.13269.83680

Provincie Noord-Holland 2017a. Natura 2000 beheerplan Noordhollands Duinreservaat 2018-2024. Provincie Noord-Holland, Haarlem, the Netherlands.

Provincie Noord-Holland 2017b. Natura 2000 beheerplan Kennemerland-Zuid 2016-2022. Provincie Noord-Holland, Haarlem, the Netherlands.

Siivonen, Y. & T. Wermundsen 2008. Characteristics of winter roosts of bat species in southern Finland. Mammalia 72 (1): 50-56. https://doi.org/10.1515/MAMM.2008.003

Speakman, J.R., P.I. Webb & P.A. Racey 1991. Effects of disturbance on the energy expenditure of hibernating bats. Journal of Applied Ecology 28: 1087-1104. https://www.jstor.org/stable/2404227

The Jamovi Project 2020. Jamovi 1.2.27 [Computer Software].

Thomas, D.W. 1995. Hibernating bats are sensitive to non-tactile human disturbance. Journal of Mammalogy 76 (3): 940-964. https://doi.org/10.2307/1382764

Verhees, J.J.F., J.C. Buys, P.H. van Hoof, H.W.G. Heijligers & W.F. de Boer 2022. Long-term trends of bats hibernating in small artificial hibernacula in northern Limburg and population dynamics explained by climatic conditions. Lutra 65 (1): 119-133.

Received: 2 November 2021
Accepted: 24 March 2022