The relationship between the numbers of hibernating brown long-eared bats (*Plecotus auritus*) and weather conditions (ambient temperatures and precipitation)

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Abstract: This study investigates the relationship between outdoor temperatures, periods of prolonged precipitation and the numbers of brown long-eared bats (*Plecotus auritus*) in hibernacula during the annual bat census. It draws on census data from three complexes: in the Amsterdamse Waterleidingduinen, the Kop van Schouwen and Klein Heidekamp, in which an average of more than ten bats were present per winter over a period of 25 years. The weather indices were examined at nine points in time prior to the day of the census (42, 35, 28, 21, 14, 7, 5, 3 and 1 day respectively). KNMI weather observations from nearby weather stations were used to calculate the mean temperature ($\bar{x}$TG), the number of (adjusted) frost days (nTN) and the sum of the negative minimum temperatures (ΣTN). In addition, the duration (ΣDR) and volume of precipitation (ΣRH) were summed for the nine periods. Pearson correlation tests were used to calculate the degree of correlation between the numbers of bats in each hibernaculum and these weather indices. It was found that more frosty days and a high cold count between 42 and 21 days prior to the count were associated with higher numbers of long-eared bats in hibernacula. Conversely, during the same periods, a negative association was found between mean outdoor temperatures and numbers of long-eared bats. No significant correlation was found between the precipitation indices and the numbers of long-eared bats in any of the hibernacula for any period prior to the census day. In conclusion, the article discusses the possible significance of some ecological adaptations by the long-eared bat to cold conditions.

Keywords: Brown long-eared bat (*Plecotus auritus*), hibernacula, mean temperature (TG), frost days, precipitation duration, precipitation amount, Pearson's correlation coefficient.

Introduction

The brown long-eared bat (*Plecotus auritus*) (here after referred to as the long-eared bat) is known as a cold-resistant bat species that usually resides in hibernacula at an ambient temperature of 2-5 °C, but which can tolerate temperatures as low as -3.5 °C for a few days (Braun & Häussler 2003). It occupies a special place among bats in Europe. Leaving aside the subspecies *P. a. begognae* of the Iberian Peninsula, *P. auritus* (sensu stricto) has one of the most extensive north-south distributions of European bats, extending across the west of the continent from central Norway (63-64 °N) (Entwistle 1999) to just south of the Pyrenees (30 °N) (Horáček & Đulić 2004, Juste et al. 2004).

Long-eared bats are known to be highly sedentary, usually with flight distances of less than ten km and further wanderings rarely exceeding 30 km (Dietz et al. 2007). Horáček & Đulić (2004) mention displacements over

Figure 1. Brown long-eared bat with ears folded under forearms and only the tragus protruding. The long guard hairs also are clearly visible. *Photo: Ben Verboom.*

Figure 2: Brown long-eared bat in hibernation with the wings partly covering the body. *Photo: Stefan Jerzykowski.*

15 km being unusual, with maximum recorded flight distances of 88 km. Long-eared bats have some special characteristics that enable them to survive conditions with low outside temperatures, up to a few degrees below freezing. The GH2 guard hairs (guard hairs with an angle between the shaft and shield) in their fur are among the longest of the West European bats and long-eared bats also have the most waves in these GH2 guard hairs (Teerink 1991): properties that provide relatively good insulation. In addition, long-eared bats almost always fold their long ears under their forearms when resting (figure 1). This position, not only limits heat loss through the ear to the environment, but also provides an extra insulating layer of air around the body. The tendency to partially drape the wings around the body in the hanging position further insulates the body (figure 2).

Movements of long-eared bats between summer habitats, such as (abandoned) buildings, tree holes or crevices, bat boxes and hibernacula are part of their phenology. Heise & Schmidt (1988) report the first finding of long-eared bats in hibernacula in Germany at the beginning of November. In general the hibernation period is between October/November and the end of March/beginning of April (Braun & Häussler 2003).

Between the autumn of 2020 and the spring of 2021, 50 bat boxes in the Veerse Bos were checked from the bottom every week. From October onwards the number of long-eared bats in the boxes gradually decreased from about 30-34 individuals to 7-10. Long-eared bats were found in the boxes during these weekly checks, except for the week of 7-12 February 2021, when the maximum temperature did not exceed 0 °C. A week later (when the temperatures were higher), ten long-eared bats were recorded in these boxes (Bekker 2022). These observations of long-eared bats gradually leaving bat boxes raises the question of where they go? A more temperature-buffered tree hollow in the forest, a nearby building or other unknown hibernacula? Lichačev (1980,

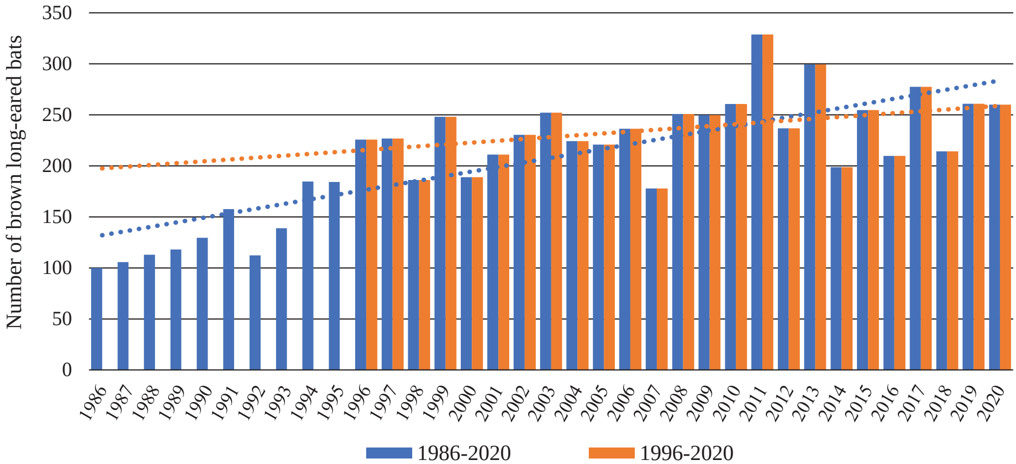


Figure 3. Trends of hibernating brown long-eared bats in the Netherlands.

in: Horáček & Đulić 2004) mentions that prolonged periods of precipitation, in combination with cold periods in the autumn, could play a role in the moment when long-eared bats leave their summer habitats. The gradually decreasing numbers of long-eared bats in bat boxes in autumn could be influenced by the lower mean outside temperature or periods with high precipitation. Conversely, the number of long-eared bats counted in hibernacula could possibly be directly related to the weather conditions (cold and/or precipitation) preceding the count. This study tests this theory with the initial hypothesis that a mean lower outside temperature prior to the census, is associated with more long-eared bats being counted in hibernacula. Secondly it is hypothesized that long-eared bats respond to previous frost periods by congregating in hibernacula in greater numbers. Finally, a third hypothesis is tested: that long-eared bats congregate in hibernacula in greater numbers after high and prolonged precipitation.

Material and Methods

Stable population

In order to test these hypotheses, it is important to assume a more or less stable population of long-eared bats over time. The national trend of long-eared bats in the Netherlands shows that in the period 1986 to 2019/2020 there was an average increase of two and a half to three times (source NEM, La Haye & van der Meij 2022, in this issue) (figure 3). The trend over 25 years, from 1996 up to 2020, is noticeably flatter, as shown by a comparison of the trend lines for the periods 1986-2019/2020 ($y=4.3661x + 128.68$) and 1996-2019/2020 ($y=1.62x + 199.17$). Therefore, in this study the correlation is studied over this shorter period of 25 years.

Hibernacula

Hibernacula were selected based on the presence of on average at least ten long-eared bats per winter over a 25-year period, with (at least) one counting taking place in each of these years, on a known census day for each year. Based on these criteria, the number of hibernacula in the three study locations are shown in table 1. The characteristics of the hibernacula in the Klein Heidekamp cellar complex are described in Glas & Kaal (2022, in this issue). The bunker complexes in Amsterdamse Waterleidingduinen and in the Kop van Schouwen are detailed in Lange et al.

Table 1. Characteristics of selected winter roosts. KVS: bunkers in Kop van Schouwen, AWD: bunkers in Amsterdamse Waterleidingduinen and KHK: cellars in Klein Heidekamp.

	Number of locations	Earliest-median and -last census dates (total census period)	Average number of brown long-eared bats
AWD	70	10-Jan.-16 Jan.-25 Jan. (16 days)	22.4
KVS	58	19 Dec.-27-Dec.-30 Dec. (12 days)	32.5
KHK	4 (+30*)	13 Jan.-22 Jan.-30 Jan. (18 days)	14.6

* there are around 30 hibernacula in the immediate vicinity of Klein Heidekamp.

(2022) and Mostert et al. (2022), respectively, both in this issue). Permission was obtained from the census leaders of these hibernacula to use the census data. Notably, the median of the census data for the Amsterdamse Waterleidingduinen and Klein Heidekamp are respectively 20 and 22 days later in the winter than those from the Kop van Schouwen.

Weather conditions

It is not known how quickly long-eared bats react to changing weather conditions and how long it takes for a long-eared bat, arriving from a summer or autumn habitat, to move into a hibernaculum. Therefore, the weather variables for a number of different days prior to the count were analysed, using nine periods of different durations prior to the days of the census: 42 days, 35 days, 28 days, 14 days, 7 days, 5 days, 3 days and 1 day. To this end we collected the observations of temperatures and precipitation from the KNMI stations closest to the hibernaculas' locations: Schiphol (weather station no. 240) for the Amsterdamse Waterleidingduinen, Vlissingen (no. 310) for the Kop van Schouwen and Deelen (no. 275) for Klein Heidekamp.

A complete list of climate variables, together with the international abbreviations used here and their definition, can be found on the KNMI website. Different methods were adopted to quantify the coldness of a winter over different periods of time. First, the mean temperature (TG) was determined over different periods prior to the day of the census. Secondly, the number of days on which the minimum temperature (TN) dropped below 0^{o} Celsius over the various periods was determined, referred to here as the (adjusted) number of frost days. Thirdly the sum of the negative minimum temperatures (TN) was determined over the relevant periods. This sum of negative temperatures, which omits the minus sign, is referred to as the 'cold number' (ΣTN). In this study, the definition of the terms 'frost days' and 'the cold number' deviates somewhat from the standard: first of all, the duration over which the numbers of frost days and the cold number are calculated is limited to the days preceding the census, as opposed to the end of the meteorological winter. In addition the ΣTN calculation, is based on the minimum temperature (TN) on each day, rather than the mean temperature (TG) over 24 hours. To quantify periods of 'long-term precipitation' the variables duration (DR) and the amount of precipitation (RH) were used. The precipitation duration (DR), expressed in units of 6 minutes per day, and the precipitation amount (RH), expressed as the 24-hour sum of precipitation, were added annually and per period.

Statistics

The Pearson correlation test was used to calculate the degree of correlation between the numbers of long-eared bats per winter home on each census and the indices for cold and precipitation. The outcome, the *r*-value, is a variable that can vary between 1 (positive = complete correlation) and -1 (negative = completely negative correlation). The terminology of Van Heijst (2022) is used to indicate the correlation strength: very low or barely present (r=0-0.3); low or weak (0.3-0.5); moderate (0.5-0.7); high or strong (0.7 and 0.9) and very high or strong (0.9-1.0). In addition to the r-values, the P-values associated with the specific correlation were calculated in Excel®, using the Student T-distribution (2-tailed). This allows one to conclude whether or not the determined correlation value is significant. The results (the r-values) of the weather indices are presented in figures with all the available results of the Pearson correlation tests for the hibernacula. These figures are always comparable, with the X-axis showing the periods over which the relationships have been calculated (42 days, 35 days, etc. up to and including one day prior to the census) and the Y-axis the extreme values within which r is located (from -1 to +1).

Results

The relationship between the numbers of hibernating long-eared bats and the weather indices for the nine different periods prior to the census days in the years 1996-2020, on the three different complexes of hibernacula are summarized in the table 2. The significant differences for each weather variable are explained below.

Mean temperature

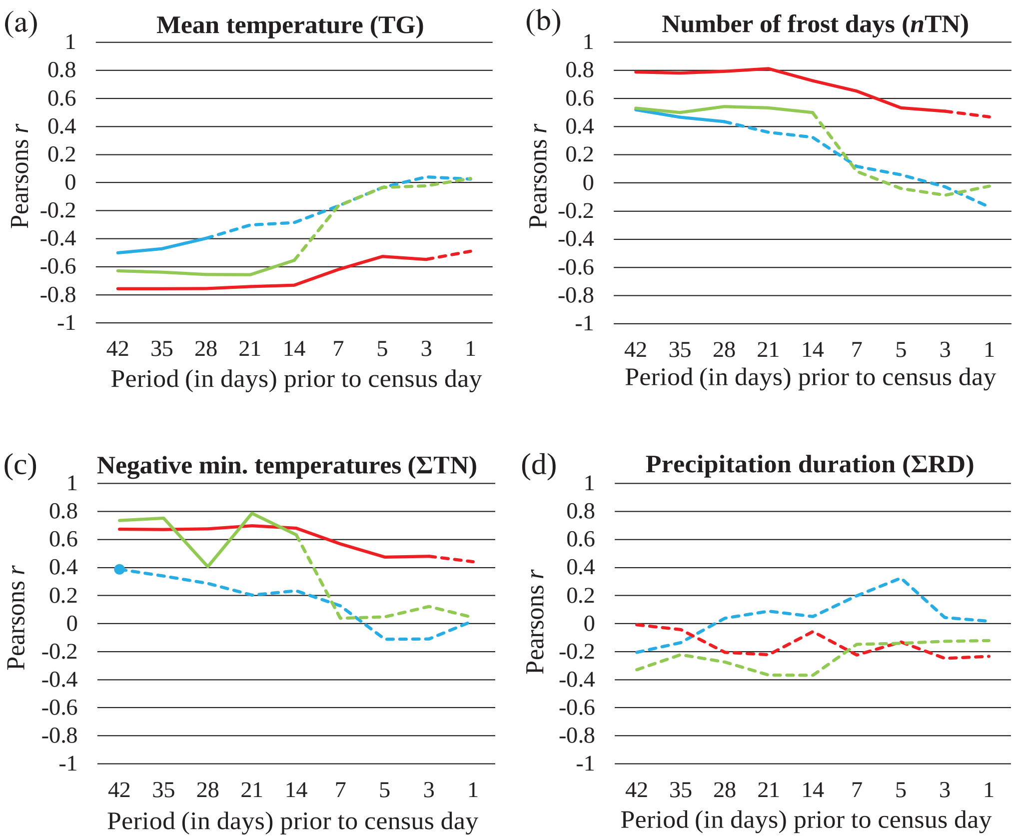
The results show that a higher mean temperature prior to the census day is related to fewer hibernating long-eared bats and vice versa (figure 4a; details in table 2). The effect of this relationship can be seen in all three complexes, but is most pronounced in the Kop van Schouwen, where for all periods, except one day prior to the count, a pronounced negative association was found between the mean temperature and the numbers of hibernating long-eared bats (figure 4a, table 2). This (significant) coherence was not found in the complexes of Klein Heidekamp and the Amsterdamse Waterleidingduinen for the preceding periods of 7 and 21 days (figure 4a, table 2). The correlations are stronger for the longer, rather than shorter periods before the census day (figure 4a).

Number of frost days

The correlation between the annual numbers of frost days and the annual numbers of hibernating long-eared bats shows a positive correlation for periods from 42 to 28 days before the census date for all three complexes (figure 4b). For the Kop van Schouwen bunkers, the correlation is highest at 42 days (r=0.79, P<0.01) and decreases gradually up to and including 3 days before the census day (r=0.51, P<0.01). At 42 days, the correlation for the Amsterdamse Waterleidingduinen (r=0.52, P<0.01) and Klein Heidekamp (r=0.53, P<0.01) complexes is approximately the same, and is significant in both cases. In these two complexes, the association gradually decreases up to and including 28 days (r=0.44, P<0.05) and 14 days (r=0.50, P<0.01) at the two sites respectively. The correlations are stronger for the longer periods before the census day than for the shorter ones.

The sum of negative minimum temperatures

The annual sum of negative minimum temperatures prior to the day of the census and the annual numbers of hibernating long-eared bats showed the strongest correlation for the hibernacula in Klein Heidekamp and the Kop van Schouwen at 42 days (r=0.74 and 0.67 respectively, both P<0.01) (figure 4c). For the bunkers of the Amsterdamse Waterleidingduinen, the correlation was lowest at 42 days (r=0.39, P<0.05). In general, the correlations for longer periods before the census day are stronger than for the shorter periods.



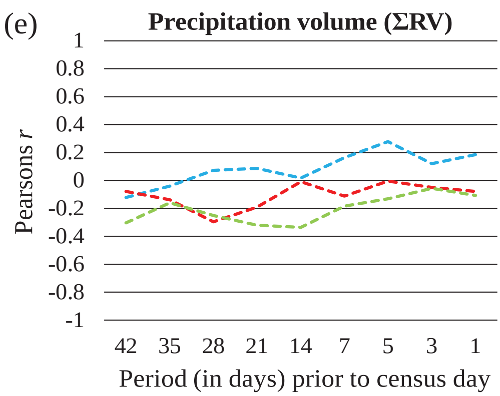


Figure 4. Correlations (expressed as Pearson's *r*) between the annual numbers of hibernating brown long-eared bats and (a) the mean temperatures, (b) the numbers of (adjusted) frost days, (c) the negative minimum temperatures (TN), (d) the total precipitation duration and (e) the cumulative precipitation volume, over nine different periods prior to the census day, in three hibernacula complexes. — the bunkers at Kop van Schouwen; — the bunkers at Amsterdamse Waterleidingduinen, and; — the cellars at Klein Heidekamp. Solid lines show a significant correlation ($P<0.05$) and dotted lines an insignificant correlation ($P\geq0.05$).

The duration and amount of precipitation

There is hardly any correlation between the total duration of precipitation for the different periods prior to the day of the census and the numbers of hibernating long-eared bats, the *r*-values are around zero or slightly negative, and are not significant ($P>0.05$). The strongest correlation was found for the bunker complex of the Klein Heidekamp, with slightly negative values ($r=0.32$, $P>0.1$) for the period 14 days before the census day (figure 4d). At

Table 2. The results of Pearson's correlation tests (Pearson's *r*) with associated significance values (P<0.01, P<0.05 and non-significant values: n.s. and *P*<0.1), for the periods of 42, 35, 28, 14, 7, 5, 3 and 1 day prior to the census day, for the Amsterdamse Waterleidingduinen (AWD), the Kop van Schouwen (KVS) and Klein Heidekamp (KHK), showing the correlation between bat numbers and: the mean temperature ($\bar{x}$TG); the number of frost days (*n*TN); the sum of negative temperatures (ΣTN); the total duration of precipitation (ΣRD), and; the total precipitation (ΣRH).

Period (in days) before census	42	35	28	21	14	7	5	3	1
AWD $\bar{x}$TG	$\bar{x}$TG-42	$\bar{x}$TG-35	$\bar{x}$TG-28	$\bar{x}$TG-21	$\bar{x}$TG-14	$\bar{x}$TG-7	$\bar{x}$TG-5	$\bar{x}$TG-3	$\bar{x}$TG-1
Pearson's *r*	-0.5	-0.47	-0.4	-0.3	-0.29	-0.17	-0.03	0.04	0.02
P-value	P<0.01	P<0.05	P<0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AWD *n*TN	*n*TN-42	*n*TN-35	*n*TN-28	*n*TN-21	*n*TN-14	*n*TN-7	*n*TN-5	*n*TN-3	*n*TN-1
Pearson's *r*	0.52	0.47	0.44	0.36	0.33	0.12	0.06	-0.03	-0.17
P-value	P<0.01	P<0.05	P<0.05	*P*<0.1	n.s.	n.s.	n.s.	n.s.	n.s.
AWD ΣTN	ΣTN-42	ΣTN-35	ΣTN-28	ΣTN-21	ΣTN-14	ΣTN-7	ΣTN-5	ΣTN-3	ΣTN-1
Pearson's *r*	0.39	0.34	0.29	0.2	0.24	0.13	-0.11	-0.11	0.02
P-value	P<0.05	*P*<0.1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AWD ΣRD	ΣRD-42	ΣRD-35	ΣRD-28	ΣRD-21	ΣRD-14	ΣRD-7	ΣRD-5	ΣRD-3	ΣRD-1
Pearson's *r*	-0.21	-0.14	0.04	0.09	0.05	0.2	0.32	0.04	0.02
P-value	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AWD ΣRV	ΣRV-42	ΣRV-35	ΣRV-28	ΣRV-21	ΣRV-14	ΣRV-7	ΣRV-5	ΣRV-3	ΣRV-1
Pearson's *r*	-0.12	-0.04	0.07	0.09	0.02	0.16	0.28	0.12	0.19
P-value	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
KVS $\bar{x}$TG	$\bar{x}$TG-42	$\bar{x}$TG-35	$\bar{x}$TG-28	$\bar{x}$TG-21	$\bar{x}$TG-14	$\bar{x}$TG-7	$\bar{x}$TG-5	$\bar{x}$TG-3	$\bar{x}$TG-1
Pearson's *r*	-0.76	-0.76	-0.76	-0.74	-0.73	-0.62	-0.53	-0.55	-0.49
P-value	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	*P*<0.1
KVS *n*TN	*n*TN-42	*n*TN-35	*n*TN-28	*n*TN-21	*n*TN-14	*n*TN-7	*n*TN-5	*n*TN-3	*n*TN-1
Pearson's *r*	0.79	0.78	0.79	0.81	0.73	0.65	0.53	0.51	0.47
P-value	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	*P*<0.1
KVS ΣTN	ΣTN-42	ΣTN-35	ΣTN-28	ΣTN-21	ΣTN-14	ΣTN-7	ΣTN-5	ΣTN-3	ΣTN-1
Pearson's *r*	0.67	0.67	0.68	0.7	0.68	0.57	0.47	0.48	0.44
P-value	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	P<0.05	P<0.05	P<0.05
KVS ΣRD	ΣRD-42	ΣRD-35	ΣRD-28	ΣRD-21	ΣRD-14	ΣRD-7	ΣRD-5	ΣRD-3	ΣRD-1
Pearson's *r*	-0.01	-0.04	-0.21	-0.22	-0.06	-0.22	-0.13	-0.25	-0.23
P-value	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
KVS ΣRV	ΣRV-42	ΣRV-35	ΣRV-28	ΣRV-21	ΣRV-14	ΣRV-7	ΣRV-5	ΣRV-3	ΣRV-1
Pearson's *r*	-0.08	-0.14	-0.3	-0.19	-0.01	-0.11	0	-0.05	-0.08
P-value	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
KHK $\bar{x}$TG.	$\bar{x}$TG-42	$\bar{x}$TG-35	$\bar{x}$TG-28	$\bar{x}$TG-21	$\bar{x}$TG-14	$\bar{x}$TG-7	$\bar{x}$TG-5	$\bar{x}$TG-3	$\bar{x}$TG-1
Pearson's *r*	-0.63	-0.64	-0.66	-0.66	-0.55	-0.17	-0.03	-0.02	0.03
P-value	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	n.s.	n.s.	n.s.	n.s.
KHK *n*TN	*n*TN-42	*n*TN-35	*n*TN-28	*n*TN-21	*n*TN-14	*n*TN-7	*n*TN-5	*n*TN-3	*n*TN-1
Pearson's *r*	0.53	0.5	0.54	0.53	0.5	0.08	-0.04	-0.09	-0.02
P-value	P<0.01	P<0.01	P<0.01	P<0.01	P<0.01	n.s.	n.s.	n.s.	n.s.
KHK ΣTN	ΣTN-42	ΣTN-35	ΣTN-28	ΣTN-21	ΣTN-14	ΣTN-7	ΣTN-5	ΣTN-3	ΣTN-1
Pearson's *r*	0.74	0.75	0.41	0.79	0.63	0.04	0.05	0.12	0.04
P-value	P<0.01	P<0.01	P<0.05	P<0.01	P<0.01	n.s.	n.s.	n.s.	n.s.

KHK ΣRD	ΣRD-42	ΣRD-35	ΣRD-28	ΣRD-21	ΣRD-14	ΣRD-7	ΣRD-5	ΣRD-3	ΣRD-1
Pearson's *r*	-0.33	-0.22	-0.28	-0.37	-0.37	-0.15	-0.14	-0.13	-0.12
P-value	n.s.	n.s.	n.s.	$P<0.1$	$P<0.1$	n.s.	n.s.	n.s.	n.s.
KHK ΣRV	ΣRV-42	ΣRV-35	ΣRV-28	ΣRV-21	ΣRV-14	ΣRV-7	ΣRV-5	ΣRV-3	ΣRV-1
Pearson's *r*	-0.3	-0.16	-0.25	-0.32	-0.34	-0.18	-0.13	-0.06	-0.11
P-value	n.s.	n.s.	n.s.	n.s.	$P<0.1$	n.s.	n.s.	n.s.	n.s.

42 days before the census date, the degree of coherence of precipitation for all the complexes varies from -0.01 to -0.33 ($P>0.1$).

Equally, no significant correlation was found in any of the complexes, for any period prior to the census day, between the amount of precipitation and the numbers of hibernating long-eared bats. Hardly any correlation was found between the amount of precipitation and the numbers of hibernating long-eared bats for the period 42 days before the census day: with the *r*-value varying from −0.08 ($P>0.1$) to −0.30 ($P>0.1$) (figure 4e, table 2). The difference between the complexes were greatest on the fifth day before the census ranging from almost -0.4 ($P>0.1$) to 0.3 ($P>0.1$), both values 'low to weak' or 'very low'.

Discussion

The Pearson correlation tests show a clear positive correlation between the number of frost days and a high cold count and the number of long-eared bats found in hibernacula. This is especially pronounced for the periods of 42 to 21 days prior to the count. This correlation was not significant in any of the complexes for shorter periods. Conversely, during the same periods, a negative association was found between mean outdoor temperatures and the numbers of counted long-eared bats.

No significant association between the duration or amount of precipitation and the numbers of hibernating long-eared bats was found. The difference between the outcome of the precipitation indices in this study and the relationship reported by Lichačev (1980) for the Moscow area may be explained by the stronger influence of the continental climate in the Moscow area, almost certainly leading to early autumn periods of precipitation being accompanied by frosty days, when summer roosts are abandoned. In autumn (calculated from the beginning of October to the end of December), the period when long-eared bats leave their summer habitats for hibernacula, the mean temperature in the Netherlands appears to high enough to allow long-eared bats sufficient opportunity to continue to forage outside during periods of precipitation. This may explain why part of the long-eared bat population only moves to hibernacula at a later stage in the autumn or after the start of winter. In the absence of low temperatures in the winter period, part of the population may not even move to hibernacula at all.

The differences between the three complexes in the degree of correlation between the numbers of hibernating long-eared bats and the cold indices are probably due to differences in local conditions. The combination of mature trees in the Slotbos in Haamstede (with many potential colony trees for long-eared bats) in the immediate vicinity (<500 m) and the relatively isolated location of the Kop van Schouwen bunker complex (which, on the eastern side mainly consists of an agricultural landscape, without forests, and surrounded on the other sides by the salt waters of the North Sea, Grevelingen and the Oosterschelde) can explain the significant positive relationship that was found between cold weather variables and the numbers of hibernating long-eared bats for shorter periods than at the other sites. Under these circumstances, long-eared bats may respond more quickly to changing weather conditions, i.e. periods of frost, by moving to the bunkers. Less than 500 m from the bunker complex in the Amsterdamse

Waterleidingduinen, there are less bulky trees with hollows or fissures, while the inner dune forests (Leyduin, Vinkenduin and Woestduin) are more than 1.5 km away. The cellar complex at Klein Heidekamp is located in the middle of a forest that has recently emerged on a heathland and also there are few old trees with holes or cracks in the immediate vicinity. There are also extensive forested areas in the area, such as the Deelerwoud, about 1 km away.

Long-eared bats in the Netherlands do not always exclusively hibernate in underground winter roosts; Jansen & Buys (1997) also mention church towers as winter roost. The presence of tree holes in the neighbourhood may also provide important hibernacula for long-eared bats (Dietz et al. 2007). A series of incidental observations confirm that long-eared bats very occasionally reside in well-insulated tree holes in winter (Macdonald & Barrett 1993). Aulagnier et al. (2009) also mention tree holes as hibernacula in areas with a temperate climate. Mostert (1997) also established that some long-eared bats spend the winter in tree crevices in the Netherlands. There are also several observations from Belgium of long-eared bats occupying tree holes and cracks, in the winter period, even during light frosts and snow (personal communications, Bob Vandendriessche and Marc Van De Sijpe). It is not clear why part of a population of long-eared bats in the western part of the distribution area, such as the Netherlands and Belgium, tends to stay in tree cavities or bat boxes during the winter period, with the exception of severe frost periods. This might be related to obtaining a favourable position for swarming sessions in spring, an important swarming period for the species (Furmankiewicz & Altringham 2007). There are concrete indications that this subpopulation is mainly composed of males: for example, in the Kop van Noord-Holland, during the winters of 2006 to 2020, seven long-eared bats, including at least six males, were found in bat boxes, as long as it did not freeze severely for at least 14 days beforehand (personal communication, Jan Boshamer). Horáček & Ðulić (2004) mention rock crevices as places that are mainly occupied by male long-eared bats in autumn, as well as spring and that these can serve as potential mating sites. Slit-shaped roosts, such as cracks in trees, loose, protruding tree bark and perhaps also nest and bat boxes give long-eared bats direct contact with the outside world allowing them to react more swiftly to the first signs of spring.

How can these results be explained alongside the findings, outlined in the introduction, that over the winter period the number of long-eared bats in bat boxes decreases, although they remain almost permanently present? A possible explanation is that in the course of the weeks preceding the regular bat census, the majority of long-eared bats leave the bat boxes for regular hibernacula, but some remain in boxes and (tree) holes or cracks that offer relatively good temperature buffering. During periods of frost that last for a few days, when the maximum daytime temperature does not exceed 0° Celsius, these last long-eared bats also leave for the hibernacula. It is quite possible that the tree holes, cracks, bat boxes and possibly also church attics in the immediate vicinity of summer roosts continue to play a role in swarming sessions in the autumn period. In this context it is significant that long-eared bats are almost absent from swarming sessions at the entrances of hibernacula such as the marl quarries in Zuid-Limburg (van Schaik et al. 2015).

Other articles in this issue describe the positive correlation between the numbers of other species such as Daubenton's bats (*Myotis daubentonii*) and Natterer's (*M. nattereri*) found in hibernacula and low outside temperatures van Zuijlen & Groenendijk 2022, Verhees et al. 2022, both in this issue. Further research could help show how these other species relate to temperature (and precipitation) variables over different periods prior to the bat census.

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