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REVIEW

# Use of synanthropic roosts by bats in Europe and North America

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## ABSTRACT

1. Diurnal roosts are vital to bats and growing evidence suggests that bats increasingly exploit synanthropic structures, such as buildings. The use of synanthropic roosts (SRs) has been explained as a consequence of the decreased availability of natural roosts imposed by habitat destruction, although growing evidence suggests that the use of SRs may be beneficial to bats in many ways, including enabling the expansion of distributional ranges.
2. Based on data from Europe and North America, our study aimed to (1) analyse the proportion of use of synanthropic vs. natural roosts, (2) test the hypothesis that bats are forced to use SRs in response to the destruction of natural habitats, (3) analyse latitudinal variation of the proportion of use of SRs and (4) address the highly contrasting pattern in the proportion of use of SRs between the two continents in the light of historical aspects of coexistence between bats and humans.
3. We compiled published data on day roosts obtained by means of radio-telemetry, providing unbiased evidence of the proportion of synanthropic and natural roosts. We compared the obtained patterns between the two continents, analysed the relationship between the proportion of use of SRs, land cover and latitude and analysed historical reconstruction of anthropogenic land use.
4. In Europe ($n$=3385 roosts), SRs were used by twice more (26) bat species and were used 17× more frequently than in North America ($n$=6795). We found no support for the hypothesis that bats use SRs in response to habitat destruction. The use of SRs increases with latitude in Europe, but not in North America, despite decreasing areas of human-altered habitats.
5. Historical processes related to the length of coexistence between bats and humans on both continents, rather than the current state of nature, may underlie the contrasting patterns observed.

 

## INTRODUCTION

Bats spend over half their lives in day roosts and, therefore, roosts represent a crucial resource to them (Kunz 1982). Given their high species diversity, mostly cosmopolitan distribution and special thermoregulatory needs, bats have adapted to the use of a vast diversity of natural day roosts such as caves, tree cavities, foliage, rock fissures, bird and termite nests, mammalian dens, leaf litter or even a specialized insect traps of carnivorous plants (Kunz & Lumsden 2003). While some species are roost generalists occupying many different types of roosts, others are adapted for using one particular roost type. The former case is, for example, represented by a neotropical species *Artibeus jamaicensis* which roosts in caves, tunnels, tree cavities, man-made structures and foliage (Ortega & Castro-Arellano 2001), while Malagasy *Myzopoda aurita* roosts exclusively in folded leaves of Ravenala palm (Ralisata et al. 2010), thus representing an extremely specialized roosting strategy. Whether they are roost generalists or roost specialists, bats always select roosts providing them with safety from predators and optimal microclimate, supporting their special thermoregulatory physiological adaptations (Speakman & Thomas 2003).

Apart from using natural roosts, bats are known to find shelter in a variety of man-made structures, such as tunnels, abandoned mines and, by far most frequently, buildings (Kunz & Reynolds 2003, Voigt et al. 2016). The use of anthropogenic roosts has often been hypothesized to be a consequence of the destruction of natural habitats resulting in a lack of natural roosts which forces bats to use man-made structures (Kunz 1982, Brigham 1991, Kunz & Reynolds 2003). On the other hand, there is increasing evidence that bats may benefit from using roosts in buildings as these provide long-term stability, safety from predators, space and suitable microclimatic conditions (Voigt et al. 2016). Buildings may have originally enabled many cave- and rock-dwelling bats to extend their northern distributional range and colonize northern regions of Europe and North America devoid of natural roosts with suitable microclimate for reproduction (Horáček 1984, Michaelsen et al. 2013, Uhrin et al. 2016, Ancillotto et al. 2016) or hibernation (Shively & Barboza 2017).

Although the use of buildings for roosting has been reported at least in 39 of 47 and 34 of 45 bat species occurring in Europe and North America, respectively (Wilson & Ruff 1999, Dietz et al. 2009, Harvey et al. 2011, Dietz & Kiefer 2016, Wilson & Mittermeier 2019), the true proportion of usage of buildings (i.e. the proportion of roosts in buildings vs. natural roosts), in particular bat species, has never been explored. This fact is understandable because except for few cave-dwelling species, which typically form large colonies and are relatively easy to detect, natural roosts of the vast majority of bat species are extremely hard to locate. Most information on their roosts thus comes from accidental findings reported by public or by targeted surveys of potential bat roosts in buildings (e.g. Mazurska & Ruczyński 2008, Spitzenberger & Weiss 2012, Sachanowicz & Wower 2013, Fagan et al. 2018, Froidevaux et al. 2020). The fact that building roosts in such surveys have been located by *a priori* search entails a strong systematic bias towards the presence of bats in this type of roost.

A recent boom in using miniaturized radio-transmitters to follow even the smallest bats has provided an increasing number of detailed studies on roosting behaviour of bats worldwide, including information on the types of structures bats use for roosting (Kunz & Lumsden 2003, Clerc et al. 2021, this study – see Appendix S1). Typically, bats are captured at their foraging sites, equipped with radio transmitters, released and followed for a few days to a few weeks to their foraging sites and day roosts (Amelon et al. 2009). Such a method provides reliable information on roost use devoid of bias caused by *a priori* search for roosts in potentially suitable structures. A proportion of natural and anthropogenic roosts found using radio-tracking studies may thus show a closer and unbiased insight into this topic.

In this review, we aimed to gather all available data obtained with the use of radio telemetry on the proportion of occupancy of natural vs. anthropogenic day roosts by bats in Europe and North America (north of Mexico). Furthermore, we addressed a possible link between the level of human-caused habitat alteration and urbanization and the intensity of using synanthropic roosts (SRs) by bats. Specifically, we tested the hypothesis that bats are forced to use SRs in reaction to the decreased availability of natural habitats and increased availability of anthropogenically altered habitats and explored the possibility that contrasting proportion of use of SRs by bats between the two continents could be attributed to respective differences in the level of destruction of natural habitats. Furthermore, we explored the latitudinal gradient in the proportion of usage of synanthropic vs. natural roosts, as some evidence from previous studies suggests that using SRs may help bats cope with harsh environments at high latitudes and expand their range to formerly uninhabited areas. Last but not least, we explored the historical processes that may elucidate a highly contrasting pattern in the use of SRs between the two continents.

## METHODS

We restricted our analysis to Europe and North America (north of Mexico) as these two regions have the longest history of bat research, their fauna have similar species richness and taxonomic composition (e.g. vast majority of species belongs to the family Vespertilionidae among which the most species rich are *Myotis* bats) and, despite many local specificities, both regions encompass roughly similar gradient of bioclimatic and vegetation zones of the northern hemisphere.

For the purpose of this study, we defined SRs as above-ground structures constructed by humans, typically buildings and other constructions such as bridges, made of stone, concrete, bricks or wood. Hereafter, we refer to all such structures as SRs or buildings, with both terms having synonymous meanings. We did not evaluate underground sites resulting from mining or quarrying as these are sometimes hardly distinguishable from natural structures and often not well distinguished in the literature.

We surveyed all radio-tracking studies in the scientific literature, including peer-reviewed papers, theses and technical scientific reports (hereafter 'papers') in the Web of Science and Google Scholar using the combination of terms 'roost', 'bat', 'chiroptera', 'radio-tracking', 'telemetry' plus Latin and common names of all species known to occur in Europe and North America (*sensu* Wilson & Mittermeier 2019). We further checked all the references contained therein until no new item was found. All the information in this review is based on papers published from 1983 to 5 August 2023. We used data only from papers where authors explicitly provided information on bat species, number of radio-tracked individuals (we used only number of bats of which roosts were located, not all bats fitted with transmitters), number and type (whether natural or man-made) of day roosts used by radio-tracked bats and geographic location of the study area. Apart from peer-reviewed papers, we used information from non-peer-reviewed reports because information on whether a roost is a building or natural is very simply distinguishable and could be hardly misidentified. Our final selection included 107 papers from Europe and 132 papers from North America (see Appendix S1). The mean number of studies per bat species was 4.7 ± 3.9 (mean ± SD, range: 1–18, median: 3) and 5.4 ± 5.6 (range: 1–27, median: 3) for Europe and North America respectively. The geographic representation of study locations included in the final set of papers is shown in Fig. 1. Study locations covered roughly similarly long latitudinal gradients of *c.* 30° between the southernmost and the northernmost sites in both continents (Europe: *c.* 35–69° N, North America: 26–56° N) and due to the latitudinal asymmetry in the distribution of climatic zones and zonobiomes between Europe and North America (e.g. Loidi et al. 2022) they encompass corresponding types of vegetation zones from arid habitats in the south to boreal forests in the north.

The differences in the proportion of SRs to natural roosts (hereafter referred to as the 'proportion of use of buildings' or 'proportion of use of synanthropic roosts') used by bats between Europe and North America were tested using Mann–Whitney *U* test because of the absence of normality in the data distribution. The proportion of roosts in buildings in each bat species was used as a replication unit in this analysis.

To analyse the proportion of natural vs. human-altered habitats in study areas, we used a GIS-based approach. For each study location, the land cover composition was calculated within two buffer radiuses (10 and 50 km) using the 'buffer' command in ArcGIS 10.8.1 (ESRI 2020). Then, the percentage of each land cover category within the buffer was calculated. The land cover map used for the extraction of land cover types was the Global Land Cover by National Mapping Organizations (GLCNMO). GLCNMO is geospatial information provided in raster format, which classifies the status of land cover of the whole globe into 20 categories (e.g. broadleaf evergreen forest, broadleaf deciduous forest, needle-leaf evergreen forest, needle-leaf deciduous forest, mixed forest, tree open, shrub, herbaceous, herbaceous with sparse tree/shrub, sparse vegetation, cropland, paddy field, cropland/other vegetation mosaics, mangrove, wetland, bare area consolidated (gravel, rock), bare area unconsolidated (sand), urban, snow/ice and water bodies). The GLCNMO data cover the whole

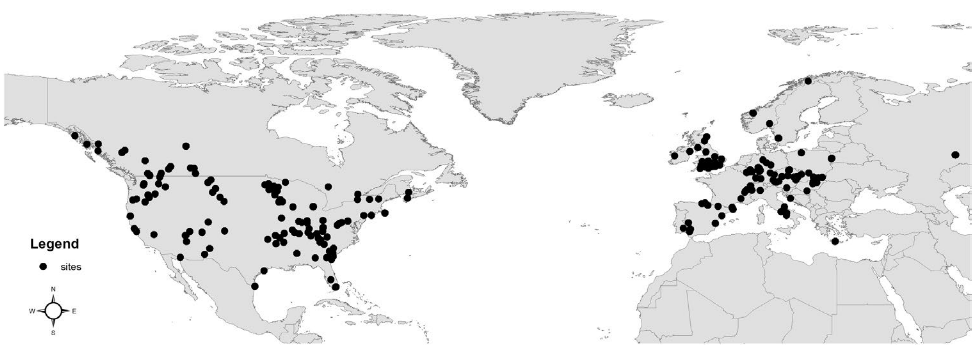


**Fig. 1.** Locations of studies included in the present analysis.

globe in grids of 500 m (15 s) intervals (Kobayashi et al. 2017).

In most papers, a study area was explicitly georeferenced or described in detail so that we were able to obtain coordinates with a precision of <5 km. In a small part of the studies (<10%), the study location was given with lower precision (<30 km). Therefore, using correlation analyses, we checked relations between proportions of the same pooled land use classes as in our study (see below) between 10 and 50 km circular buffer areas obtained from studies with accurate study locations and we found out that the respective class types are highly correlated (Spearman $R$: 0.47–0.85, $P<0.001$) so that we decided to use 10 km circular area land use classes as these had good informative value. An area of this size is a biologically meaningful value because it is roughly an area that most species of insectivorous bats cover during their flight activity (Laforge et al. 2021).

Prior to analysis, we aggregated data onto five land cover categories (hereafter referred to as 'main land cover types'): *natural habitats* (= aggregated land cover classes: broadleaf evergreen forest, broadleaf deciduous forest, needle-leaf evergreen forest, needle-leaf deciduous forest, mixed forest, tree open, shrub, herbaceous, herbaceous with sparse tree/shrub, sparse vegetation, mangrove, wetland, bare area, consolidated (gravel, rock), bare area, unconsolidated, snow/ice and water bodies), *forests* (= aggregated land cover classes: broadleaf evergreen forest, broadleaf deciduous forest, needle-leaf evergreen forest, needle-leaf deciduous forest and mixed forest), *cropland* (= aggregated land cover classes: cropland, paddy field and cropland/other vegetation mosaic), *urban habitats* and *human-altered habitats* (= aggregated *cropland* and *urban habitats*).

To analyse the relationship between the proportion of use of buildings by bats and main land cover types, we used generalized linear models (GLM) with quasi-binomial distribution of errors in R software, version 4.1.2 (R Core Team 2021). The ratio of all roosts in buildings to all roosts found in a given study location was used as the dependent variable, and the land cover variables were used as predictors in separate models. All $P$-values were corrected using the Benjamini–Hochberg procedure which controls for False Discovery Rate due to multiple tests (Benjamini & Hochberg 1995). To test for differences in the area of human-altered and natural habitats within 10 km circular buffers around study sites between the two continents, we used Mann–Whitney $U$ test because of the absence of normality in the data distribution.

To explore long-term historical patterns in the coexistence of bats and buildings, we downloaded, plotted and visually checked historical data covering the whole Common Era derived from archaeological evidence, modelling (for historical times) and direct measurements (for the most recent times) on the development of anthropogenic land cover types, including area of built-up areas, pastures and cropland (Klein Goldewijk et al. 2017) for Europe (available only excluding Russia), United States and Canada, and aggregated data from the latter two countries to get summary data for the whole of North America. The data were downloaded from https://archaeology.datastations.nl/dataset.xhtml?persistentId=doi:10.17026/dans-25g-gez3 as available on 1 November 2023. To obtain comparable data, we expressed the relative representation of built-up areas for each continent as its proportion (%) of the total area for each continent.

## RESULTS

We compiled data on 3385-day roosts used by 2263 individuals of 31 bat species (66% of local bat fauna) in Europe and 6795-day roosts used by 3095 individuals of 33 bat species (73%) in North America. The mean number of day roosts per bat species was 109.1 ± 177.4 (mean ± SD, median: 35, range: 3–876) and 205.9 ± 288.4 (median: 87, range: 2–1167) for Europe and North America respectively.

The two study regions significantly differed in the proportion of SRs used by bats ($Z=4.567$, $P<0.0001$, $N_{\text{Europe}}=31$, $N_{\text{North America}}=33$). While SRs made up 38% of all roosts found in Europe, it was only 2.2% in North America. At least 1 day roost in a building was found in 26 of 31 (84%) and 13 of 33 (39%) bat species studied in Europe and North America respectively. In Europe, four of the studied species (*Pipistrellus kuhlii*, *Pipistrellus pipistrellus*, *Plecotus austriacus* and *Rhinolophus ferrumequinum*) had 100% and further 10 species had well over 50% of all their roosts in buildings. In contrast, there was only one species (*Eumops floridanus*) having 100% of roosts in buildings in North America, in five species (*Eptesicus fuscus*, *Myotis yumanensis*, *Myotis lucifugus*, *Myotis occultus* and *Corynorhinus townsendii*), the building occupancy ranged between 10% and 24%, and in further seven species it was less than 1.1% (Fig. 2).

If we restrict our comparisons to genera *Eptesicus* and *Myotis*, which occur on both continents, to avoid possible taxonomic bias, we get quite similar results: SRs were used by 83% of species from Europe vs. 50% in North America, and 47% of all roosts used by European species were in buildings vs. only 3.1% in North America.

### Land cover vs. proportion of use of buildings

In most cases, we found no relation between the proportion of major land cover types at the study sites and the proportion of use of buildings by bats neither in Europe

 

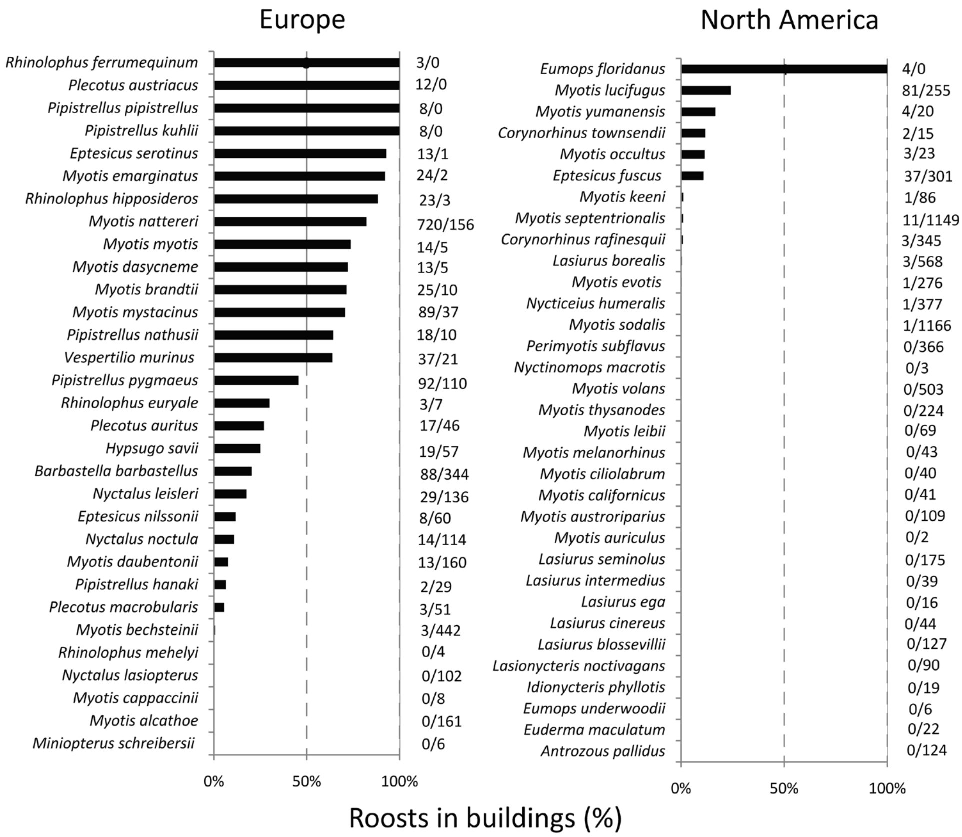


**Fig. 2.** Proportions of synanthropic to all diurnal roosts used by bats in Europe and North America as reviewed based on 239 papers reporting on roost types used by radio-tracked bats. Right from the graphic representation of each species are values showing the number of synanthropic roosts/number of natural roosts compiled from the published information.

**Table 1.** Parameter estimates from analysis of the relationship between the proportion of use of synanthropic roosts and main land cover classes using GLM with quasi-binomial link function

| | Effect of land cover on the proportion of roosts in buildings | | |
|---|---|---|---|
| | Estimate | SE | $P_{adj}$ |
| Europe | | | |
| Intercept | −1.701 | 0.204 | 0.000 |
| All natural habitats | 0.007 | 0.006 | 0.249 |
| Cropland | −0.020 | 0.008 | 0.013 |
| Urban habitats | 0.011 | 0.007 | 0.130 |
| Forests | 0.002 | 0.006 | 0.709 |
| North America | | | |
| Intercept | −3.843 | 1.262 | 0.003 |
| All natural habitats | −0.013 | 0.017 | 0.443 |
| Cropland | 0.008 | 0.019 | 0.665 |
| Urban habitats | 0.058 | 0.042 | 0.163 |
| Forests | −0.020 | 0.015 | 0.170 |

nor in North America (Table 1). The sole exception was a negative relation between an area of cropland and the proportion of use of buildings.

However, the two regions significantly differed in the proportion of the main land cover types in the study areas. Europe had significantly less natural habitats ($Z=-5.980$, $P<0.001$) and less forests ($Z=-2.542$, $P<0.05$), but more cropland ($Z=5.978$, $P<0.001$) and urban habitats ($Z=5.286$, $P<0.001$, Fig. 3). On average, Europe had almost twice more human-altered habitats (urban plus cropland) at the study sites than North America (Europe: 43.0 ± 29.0% and North America: 23.3 ± 27.2%).

## Latitudinal gradient, land cover types and the proportion of use of buildings

The proportion of use of SRs significantly increased with latitude in Europe (slope = 0.149, $P<0.001$, Kendall Tau = 0.155, Fig. 4), but not in North America (slope = 0.089, $P=0.266$, Kendall Tau = 0.055). The area of all natural habitats, including forests, increased with increasing latitude, the area of cropland decreased and urban habitats showed no trend in Europe (Table 2). In North America, there was no latitudinal trend in major habitat types, except for

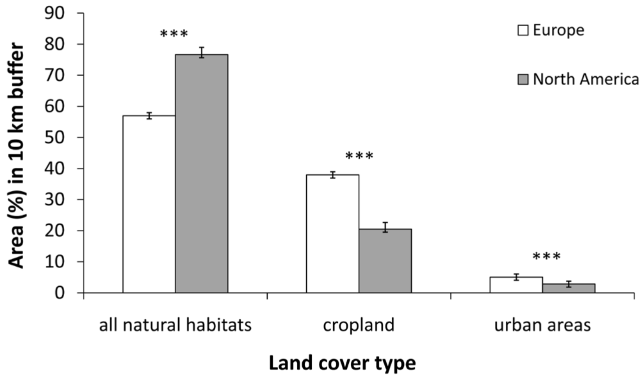


**Fig. 3.** Comparisons of the area of main land cover types present around study locations where data on roost types were collected. Asterisks above each pair of columns refer to statistical significance ($P<0.001$) as obtained using Mann–Whitney $U$ test.

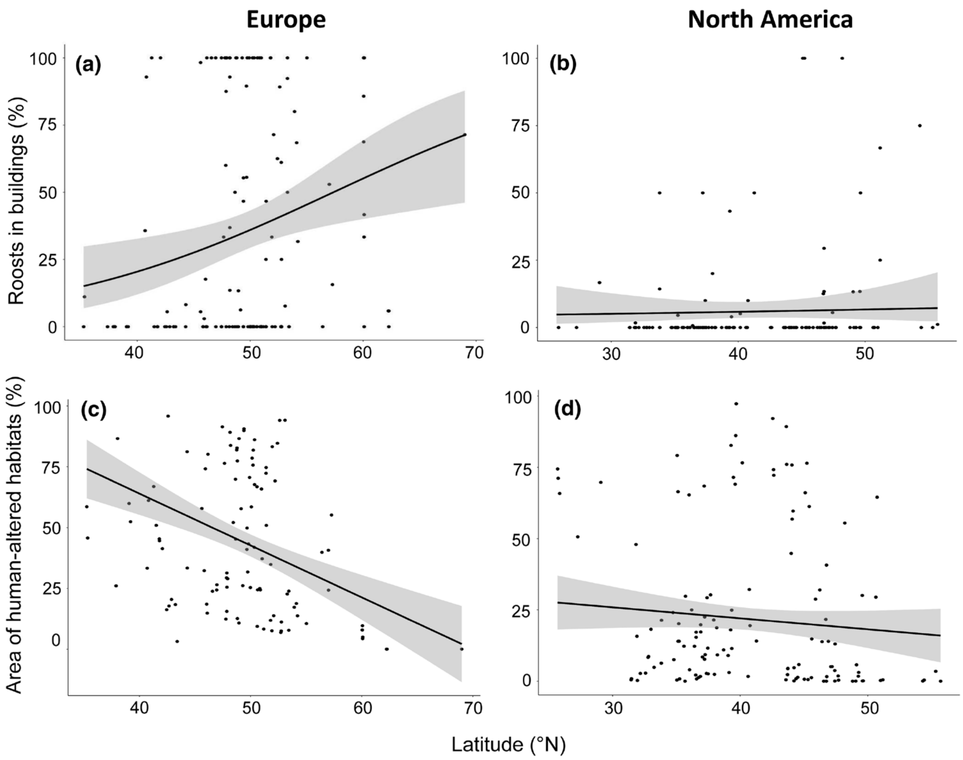


**Fig. 4.** Relationship between the proportion of synanthropic roosts (a, b) and the proportion of area of human-altered habitats (c, d) and latitude in Europe. Regression curves depict GLM regression models with quasi-binomial distribution of error; grey areas are 95% confidence intervals. While both relationships are highly significant ($P<0.001$) for Europe, they are not significant for North America.

urban habitats, which decreased with latitude. Overall, the area of all human-altered habitats significantly decreased towards the north in Europe, but not in North America.

## Historical aspects of coexistence between bats and humans

Based on data on the historical reconstruction of anthropogenic land use (Klein Goldewijk et al. 2017), we visualized and analysed the temporal development of relative representation of areas covered with built-up space and total area of human-altered habitats in Europe and North America during the Common Era. It clearly shows almost a millennium-long difference in the onset of rapid growth of built-up areas between Europe and North America (Fig. 5) and an even longer temporal difference in the onset of alteration of natural habitats to anthropogenic ones (Appendix S2).

**Table 2.** Parameter estimates from analysis of latitudinal variation of main land cover classes in 10 km buffer area around study locations in Europe and North America using GLM

| | Effect of latitude on land cover | | | | | |
|---|---|---|---|---|---|---|
| | Slope | Sum Sq | Mean Sq | d.f. | $F$ | $P_{adj}$ |
| Europe | | | | | | |
| Land cover class | | | | | | |
| Urban | −0.252 | 292.000 | 291.700 | 1 | 0.916 | 0.340 |
| Cropland | −1.837 | 15514.000 | 15513.500 | 1 | 23.733 | <0.001 |
| Forests | 2.378 | 25994.000 | 25993.900 | 1 | 35.313 | <0.001 |
| All natural habitats | 2.089 | 17783.000 | 17782.800 | 1 | 22.076 | <0.001 |
| North America | | | | | | |
| Land cover class | | | | | | |
| Urban | −0.254 | 495.100 | 495.070 | 1 | 8.019 | <0.01 |
| Cropland | −0.009 | 1.000 | 0.570 | 1 | 0.001 | 0.976 |
| Forests | −0.002 | 0.000 | 0.040 | 1 | 0.000 | 0.995 |
| All natural habitats | 0.262 | 529.000 | 529.130 | 1 | 0.766 | 0.383 |

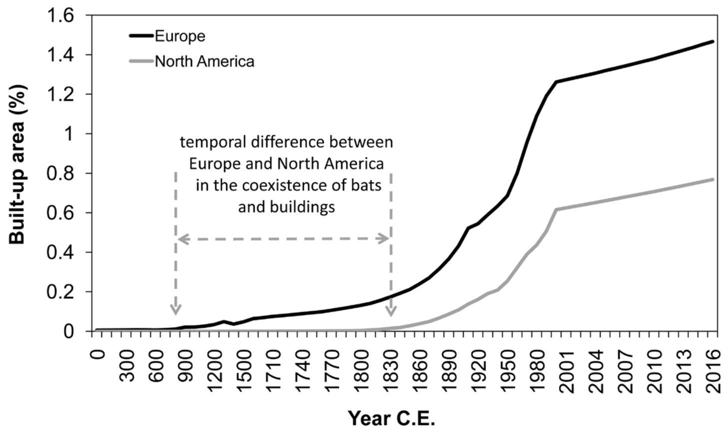


**Fig. 5.** Temporal dynamics of growth of built-up areas in Europe and North America showing roughly a millennium-long difference between the two continents in the onset of rapid growth of areas covered with human settlements. The graph is based on data on land cover reconstruction by Klein Goldewijk et al. (2017). The temporal scale is not linear due to the nature of the reconstructed data.

## DISCUSSION

This is, to our knowledge, the first review addressing the proportion of usage of synanthropic vs. natural roosts by bats in Europe and North America. Although the use of SRs by bats is widespread on both continents, our extensive dataset based on independent evidence clearly shows that about 17× higher proportion of bat populations and twice more bat species in Europe use SRs in comparison with North America. In the case of European bats, our findings are more or less in accordance with published evidence on their roosting behaviour. Most of the 14 species having more than 50% of all roosts located in buildings are ranked among those strongly dependent on man-made structures during active periods of the year (Dietz & Kiefer 2016). By contrast, *Nyctalus leisleri* and *Barbastella barbastellus* have traditionally been regarded as roost specialists selecting roosts in trees (e.g. Russo et al. 2004, Ruczyński & Bogdanowicz 2005), but our data clearly demonstrated their ability to exploit SRs, too. Among the five species with zero number of SRs, only in *Miniopterus schreibersii* occasional but rare roosting in buildings has been reported in the literature (Presetnik et al. 2009).

Among the six North American species with >10% of studied roosts located in buildings, *Myotis lucifugus* and *Eptesicus fuscus* are, by far, the most frequently reported abundant dwellers of buildings (Kunz & Reynolds 2003, Harvey et al. 2011). However, our data pinpoint that only a small part of their populations actually roost there. All the other species with positive records in buildings are generally recorded on a much rarer basis (Kunz & Reynolds 2003), which is in agreement with our findings. On the other hand, *Perimyotis subflavus* and *Antrozous pallidus* are often quoted as frequent inhabitants of buildings (at least in some regions – e.g. Wilson & Ruff 1999) but we did not find any support for that, despite quite an extensive dataset (i.e. 366 and 124 roosts found in *Perimyotis subflavus* and *Antrozous pallidus*, respectively). Few other bat species from North America, such as *Tadarida brasiliensis* and *Myotis velifer*, have been known to frequently roost in buildings (e.g. Kunz & Reynolds 2003, Li & Wilkins 2015), but there was no available study to be included in our analyses.

The profound difference in the proportion of usage of buildings by bats between the two continents could eventually be caused by phylogenetic bias, as closely related species or lineages are more likely to share common traits (such as primary roosting strategy) than less closely related taxa (e.g. De Bello et al. 2021). This particularly holds for the bats of the genus *Lasiurus* occurring exclusively in the New World, predominantly roosting in foliage (Carter & Menzel 2007), a roosting strategy absent among European bat fauna. However, our separate analysis of roost occupancy for two bat genera common for both continents, *Myotis* and *Eptesicus*, having substantial representation in both bat faunas (40% and 40% of bat fauna for Europe and North America, respectively) and among species included in our study (39% and 49% for the two respective regions), did not support this possibility. Indeed, almost twice as many species of these two genera used roosts in buildings with 15 times higher proportion of SR in Europe than in North America.

## Are bats forced to roost in buildings?

Many authors suggested that the usage of SRs by bats is an ultimate consequence of the deterioration of natural habitats, destruction of natural roosting opportunities and urbanization (Kunz 1982, Kunz & Reynolds 2003). However, we found no direct relation between the proportion of use of buildings and the proportion of available natural habitats (Lacki et al. 2007) around study locations.

On the contrary, there has been increasing evidence that change in roosting strategy from natural to SRs may provide multiple benefits to bats. Bats roosting in buildings often have more space and may form bigger colonies than in natural roosts (Lausen & Barclay 2006), are better insulated and provide better microclimate for development of juveniles (Rodrigues et al. 2003, Lausen & Barclay 2006, Johnson et al. 2019), host less parasites (Uhrin et al. 2010) and are less accessible to predators (Voigt et al. 2016). For bats that originally used tree roosts, buildings provide more permanent roosting structures (Brigham 1991, Lausen & Barclay 2006; but see Lučan et al. 2009). In large areas void of natural roosting opportunities, such as open grasslands (prairies and steppes), flat plains and deserts, roosting in buildings enabled bats to expand their distributional range (Kunz & Reynolds 2003). In historical times, many originally cave-dwelling species greatly expanded their range towards the north due to the adaptive switch in roosting strategy from caves to spacious lofts of large buildings, a situation well known in many species, such as *Myotis myotis*, *Myotis blythii*, *Myotis emarginatus*, *Rhinolophus hipposideros*, *Rhinolophus ferrumequinum* or *Plecotus austriacus* in Europe (Horáček 1984, Rodrigues et al. 2003, Dietz & Kiefer 2016) and *Myotis velifer* and *Tadarida brasiliensis* in North America (Kunz & Reynolds 2003, McCracken et al. 2018). Accordingly, the recent enormous northward shift in the distribution of *Hypsugo savii* and *Pipistrellus kuhlii* in Europe is connected with switch from natural to SRs along the whole leading edge of their range expansion (Ancillotto et al. 2016, Uhrin et al. 2016).

Our analysis of the relationship between the proportion of occupancy of SRs and the latitude showed an increasing tendency towards the north in Europe despite decreasing area of human-altered habitats, thus providing further evidence supporting the hypothesis that bats are not forced to use SRs in response of anthropogenic pressure but, rather, they may actively select this type of roosts. This could be particularly beneficial when colonizing high latitudes. Indeed, results of several studies from the northernmost extremes of distributional ranges of bats in Europe and North America concluded that roosting in buildings may have been the crucial adaptation that allowed bats to colonize such extreme regions (Michaelsen et al. 2004, Frafjord 2007, Shively & Barboza 2017).

Furthermore, it is worth mentioning that of 14 European bat species with >50% of SRs, only 1 species (*Plecotus austriacus*) shows a decreasing long-term population trend, whereby others are increasing (8 species), has a stable (2 species) or unknown or uncertain (2 species) population trends, and in the remaining 12 species, 5 are increasing, 1 is stable and 6 have uncertain or unknown trends (Arlettaz et al. 1999, Van der Meij et al. 2015, Toffoli & Calvini 2021, Bat Conservation Trust 2024). This provides further supporting evidence for the hypothesis that bats rather profit from using SRs. It is virtually impossible to link the proportion of usage of SRs with long-term population trends for bats in North America, given the lack of such information from that region, and simultaneously, due to the fact that many species using SRs have been heavily impacted by white nose syndrome, an infectious disease causing significant declines in bat populations over last two decades (Hoyt et al. 2021), thus confusing the situation.

All in all, using SRs seems to have more benefits than costs to bats. This is particularly relevant for bats in Europe, where they roost in buildings with much higher frequency, and simultaneously, most species roosting predominantly in buildings have increasing or stable population trends, despite the area of natural habitats available to them being significantly lower than in North America.

At the same time, however, SRs may be beneficial to bats only as long as they are located within reach of good foraging habitats, typically woody vegetation (Boughey et al. 2011). Such a combination is more or less common in rural landscapes but might be less frequent with increasing urban gradient. Indeed, increasing urbanization has been suggested as one of the most important factors of habitat alteration and biodiversity loss (Grimm et al. 2008, McKinney 2008). In the case of bats, however, published analyses revealed rather conflicting than unambiguous conclusions (Browning et al. 2021) among which of particular importance for the pattern found in our study are findings by Jung and Threlfall (2016), who reported on significant regional differences in the reaction of insectivorous bats to urbanization. More specifically, Jung and Threlfall (2016) found that insectivorous bats in Europe showed no association with urbanization as compared to bats in North America, which is in accordance with our findings. A growing body of literature brought a piece of evidence that urban environments in Europe can harbour rich bat populations, including many habitat specialists, if certain conditions are met, such as access to diverse tree vegetation and water bodies and low levels of light pollution (Apoznański et al. 2021, Lewanzik et al. 2022, Printz & Jung 2023). Indeed, surveys of bats in large European cities found rich bat faunas, typically comprising >60% of all bat species occurring in a given country and not differing from adjacent rural areas (e.g. Berlin, Germany – Teubner et al. 2008, Hamburg, Germany – Wiermann & Reimers 1995, Prague, Czech Republic – Hanák et al. 2009, Warsaw, Poland – Lesiński et al. 2001, Vienna, Austria – Spitzenberger 1990, Budapest, Hungary – Molnár et al. 1999). It has been demonstrated that even the top habitat specialists could thrive in well-preserved urban forests (Dietz et al. 2020), thereby stressing the importance of conservation of this type of habitat within urban matrix.

## Length of coexistence and building architecture as a driver of contrasting pattern

The study sites on the two continents significantly differed in the representation of natural and human-altered habitats with Europe having fewer natural habitats and more cropland and urban habitats than North America. However, the differences were relatively small (*c.* 2–20%) in comparison with multiple contrasts in the overall proportion of usage of SRs and could hardly stand, as a sole factor, behind the observed pattern.

The distribution of study locations was quite uneven on both continents (see Fig. 1) and one could argue that land cover data from these locations might not be representative of the whole area of each continent. However, there is no support for this hypothesis, as the mean values for main land cover types obtained from the study locations are very similar to those available for each continent from empirical measurements. For instance, total area of human-altered habitats has been oscillating around 45% and 25% in last four decades, that is, roughly the time-frame of all studies included in this review, in Europe and North America, respectively (Klein Goldewijk et al. 2017, Appendix S2), which is in good correspondence with average values from our study locations (i.e. roughly 43% and 23% for the two respective regions, see the Results section).

Although the differences in the amount of available natural habitats may have contributed to the observed contrasting pattern between the two continents, we found no convincing support for the hypothesis that bats are forced to use buildings as an alternative roosting opportunity as a consequence of the lack of natural roosts in response to habitat destruction. We assume that a more important factor than the current level of anthropogenic pressure might be the historical context, that is, the time bats have had for coexistence and/or adaptation to SRs and habitat alteration induced by humans. It is worth mentioning that bats are unique among mammals given their slow life history (Barclay & Harder 2003), including low reproductive rate, extreme longevity and generally conservative habits, which in turn may result in a long reaction time needed for adaptation to novel conditions, such as switch from natural to SRs. Although there is no doubt that bats have coexisted with human-built structures, shelters or buildings for thousands of years (e.g. Voigt et al. 2016), construction technologies and materials greatly differed between the two continents, thereby providing bats with contrasting chances and time to adapt. If we narrow the temporal focus on the Common Era, the prevailing architecture of domestic dwellings built in North America included various types of earth- or grass-covered shelters or lodges (e.g. hogans), lodges from a framework of saplings covered with sheets of bark and thatch lodges covered with grass or teepees, while buildings made of more permanent materials, such as stone or bricks, were rare and regionally restricted to few areas in south-west and north-east (Nabokov & Easton 1990). All in all, most ancient human-built structures in North America were of low durability, and given the central position of fireplace in most of these dwellings, allowing smoke to penetrate roof spaces (Nabokov & Easton 1990, Pritzker 2000), they had little potential to be used by bats for roosting. Archaeological evidence of large, complex and permanent buildings is very scarce from pre-Columbian times, suggesting that the number and density of settlements was generally low (Milner & Chaplin 2010, Munoz et al. 2014). In Europe, on the other hand, the use of bricks and stone for the construction of buildings predated the beginning of the Common Era and was widespread at least in all southern regions (Wright 2009). Moreover, a very rich and spatially dense archaeological evidence points out on widespread construction of large buildings of sacral purposes, such as temples, cathedrals or churches, which, together with domestic dwellings, could provide a plethora of potentially suitable roosting sites for bats of diverse original roosting strategies. Along with archaeological evidence, the two continents greatly differed in estimated human population density which certainly mirrored the density of human-constructed structures potentially available to bats during pre-Columbian times. While total human population estimates for the years 1, 1000 and 1500 C.E. are less than 5 M people for whole of North America, it is 34 M, 40 M and 78 M people for Europe, respectively (Bolt & Van Zanden 2020). That means, due to the much larger (*c.* 2.4×) total land area of North America in comparison with Europe, the overall density of settlements was much lower on the former continent. It was not until after the European contact that the situation dramatically changed. Then, rapid spreading of new European architecture, including the use of new construction materials, such as stone and bricks, flooded North America and introduced a variety of buildings with plenty of potential roosting sites for bats. Along with these facts, and based on reconstructed data on historical land use published by Klein Goldewijk et al. (2017), we demonstrated *c.* 1000-year-long time window between the rapid increase in built-up areas in Europe and North America, suggesting that bats in Europe had much longer time for adaptation to use buildings for roosting. Last but not least, a millennium-long temporal difference exists in the onset of intensive deforestation and anthropogenically induced habitat alteration between Europe and America (Pongratz et al. 2008, Kaplan et al. 2009, Zanon et al. 2018, Ellis 2021, Li et al. 2023, Wang et al. 2023) further advocating the significance of temporal aspect of coexistence of bats and humans, a possible cause of the observed contrasting pattern in the roosting behaviour of bats between the two continents.

## CONCLUSION

In this review, we synthesized evidence that SRs are an extremely important resource to bats in Europe, but they are used much less by bats in North America. At the same time, we found no direct relationship between the level of anthropogenically driven habitat alteration and the proportion of use of SRs, leaving no support for the hypothesis that bats are forced to roost in buildings in response to the lack of natural roosts resulting from habitat destruction. Taking this into account and regarding the profound differences in the proportion of use of SRs between the two continents, we suggest, that historical processes, rather than the recent state of nature, may explain this highly contrasting pattern. Specifically, we demonstrated and reviewed intercontinental differences in the length and intensity of coexistence between bats and humans, including ancient architecture, extent of built-up areas, population density and extent of human-induced habitat alteration that, in turn, may have been translated into different times that bats have had for adaptation to the novel types of roosts. In this context, the high proportion of roosting by bats in buildings in Europe accompanied by stable or even positive population trends of many species might be regarded as an example of a potential for coexistence between an endangered, highly specialized and diverse mammalian group and humans, when certain conditions, such as access to foraging and drinking habitats, are met. SRs should play an important role in the conservation management even in bat species which use them rarely as these rare instances may represent newly established behaviour leading to the spreading of this successful adaptation, as demonstrated by past and present range expansions in several species, including originally roost specialists (Horáček 1984, Ancillotto et al. 2016, Uhrin et al. 2016).

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## CONFLICT OF INTEREST

None declared.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

**Appendix S1.** List of bat species, their taxonomic position and references to publications used for extraction of data on the type of diurnal roosts.

**Appendix S2.** Chart depicting the temporal dynamics of growth of area of human-altered habitats in Europe and North America.