Factors influencing roost use by Short-toed Treecreepers *Certhia brachydactyla* at urban sites

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Although treecreepers *Certhia* spp. are known to roost communally, the factors associated with roost use have never been quantified. Here, we investigate the influence of environmental conditions on the roosting behaviour of Short-toed Treecreepers *C. brachydactyla* in an urban setting in The Netherlands. We performed transect-based nocturnal counts of 120 roosts on 487 days during a three-year period. We correlated total number of birds per roost per day to multiple relevant environmental factors (daily duration of precipitation, daily sum of precipitation, daily mean wind direction, daily mean wind speed, daily maximum temperature, daily minimum temperature, daily mean temperature, daily mean humidity and daylength). Numbers of roosting Treecreepers were positively associated with minimum daily temperature and northern winds and negatively with day length and maximum daily temperature. Our study shows that Treecreepers respond to short-term temperature fluctuations by altering their roosting strategy. Communal roosting in the species is thus likely a behavioural response to a combination of severe weather and short day length. Most roosts are generally vacant (86.8 ± 3.5% SD) or hold single roosting treecreepers (7.6 ± 3.9%) and a few apparently optimal sites hold consistently large numbers (6.6 ± 3.5%). Vacant roosts peak in number during the breeding season (89.5 ± 3.8% vs. 85.8 ± 2.9% in winter), whereas singleton roosts (8.0 ± 4.2% vs. 6.7 ± 2.5% in the breeding season) and communal roosts (7.3 ± 3.4% vs. 4.8 ± 3.3% in the breeding season) are most common during winter. Our study fills an important gap in our knowledge of roosting behaviour in passerine birds, but much remains to be learned.

Key words: treecreepers, *Certhia*, roosting, nocturnal behaviour, winter, urban ecology

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Communal roosting in birds occurs mainly outside the breeding season and is generally thought to be driven by multiple, not mutually exclusive, processes (Weatherhead 1983, Eiserer 1984). Roosting jointly may be a response to inclement weather conditions and may provide thermal benefits through the use of sheltered sites or through the physical proximity of conspecifics ('climatic refuge hypothesis'; Eiserer 1984). Communal roosting may also be a strategy to reduce the impacts of predation on individual birds ('threats refuge hypothesis'; Eiserer 1984). Finally, communal roosts may enhance the exchange of information on foraging locations during times of resource scarcity ('information centre hypothesis'; Ward & Zahavi 1973, Marzluff *et al.* 1996).

Communal roosting is mainly found among large-bodied and sociable birds (Beauchamp 1999) and is particularly well-studied in groups such as herons (Ardeidae; Birkhead 1973, Weseloh *et al.* 2010, Yousefi *et al.* 2019), geese (Anatidae; Béchet *et al.* 2010) and parrots (Psittaciformes; Cougill & Marsden 2004, Seixas *et al.* 2018), but this behaviour is also common in several passerine families (e.g. bushtits, Aegithalidae; swallows and allies, Hirundinidae; New World

Treecreeper roost under roof (Bergen, Noord-Holland, 13 January 2018).

black-birds, Icteridae; Starlings, Sturnidae; crows and allies, Corvidae; see Beauchamp 1999, Eiserer 1984, McGowan *et al.* 2006), where it is much less well-known. Roosts of small passerines are often notoriously difficult to locate and may have prevented systematic assessments in the past (Dhondt *et al.* 2007, O'Connell *et al.* 2023). Passerine roosting behaviour is particularly understudied during the non-breeding season (Smith *et al.* 2008), when this behaviour forms an important adaptation to adverse weather and to local foraging conditions.

Treecreepers *Certhia* spp. are known to frequently roost communally (Rankin & Rankin 1939, Mackenzie 1957, Glutz von Blotzheim & Bauer 1993). Generally, roosts of representatives of the genus are found in tree crevices, but the Short-toed Treecreeper *C. brachydactyla* is also known to frequently roost on human-made constructions, such as residential buildings. This behaviour is also at least, occasionally, seen in Eurasian Treecreeper *C. familiaris* and Brown Creeper *C. americana* (Stone 1950, Mackenzie 1959). In this case, they generally use sheltered areas under eaves, where they may roost independently from each other or communally in a huddle with only tails and backs exposed, especially during winter (Glutz von Blotzheim & Bauer 1993).

Although much anecdotal information is available on the roosting habits of treecreepers, systematic and long-term study of roosting in these widespread species is lacking. However, treecreeper roosts are relatively easy to locate on buildings, not only because they often roost fully exposed, but also because roost detection is facilitated by traces of urea left on the gables of residential buildings. This allows for the long-term tracking of the numbers of birds at multiple roosts to investigate the drivers of variability in the temporal use of roosts.

Studies focusing on the meteorological influence on bird roosting behaviour point towards the important role of roosts as thermal refuges. Short day length, snow cover and low mean temperature increase numbers of communally roosting Long-eared Owls *Asio otus* (Dobrev *et al.* 2021). Interestingly, in colder continental climates with prevailing freezing temperatures, temperature alone played a major role in communal roosting by Long-eared Owls (Kucherenko & Kalinovsky 2018). In more sunny climates, solar radiation best explained roost site selection by passerines (Villén-Pérez *et al.* 2013). Andean Condors *Vultur gryphus* select roosts sites with minimal exposure to inclement weather (Lamertucci & Ruggiero 2013). Thus, it appears that birds opportunistically choose whichever roost site offers the best thermal benefits given the local climate. Within roosts, Long-tailed Tits *Aegithalos caudatus* often actively compete for positions that are most favourable from a thermal perspective (McGowan *et al.* 2006). That this rule is not general is exemplified by Cattle Egrets *Bubulcus ibis*, which roost in lower numbers at communal roosts during poor weather conditions, mainly through cohort splitting, whereby birds seek shelter at the nearest site rather than a communal roost during bad weather (Youcefi *et al.* 2019).

Here, we study the use of roosts by Short-toed Treecreepers, a resident species strictly tied to the presence of trees (Basile *et al.* 2016, Gianpasquale 2017, Snell *et al.* 2020), during a three-year period in an urban area in The Netherlands. We performed systematic nocturnal surveys to assess the number of treecreepers roosting at each site and to describe changes in numbers over time. Because the species is known to move with ease through areas with unsuitable habitat within urban areas (Snell *et al.* 2020), we monitor a large number (n = 120) of scattered roosts, to attempt to control as much as possible for the effect of birds moving between roosts on the cumulative number of roosting treecreepers.

The systematic surveys allow us to relate roost use to meteorological factors to investigate if roost use is correlated with poor weather conditions (low temperatures, wind conditions or rainfall), supporting the climatic refuge hypothesis. We make the assumption that the huddling behaviour of treecreepers at communal roosts is primarily a behavioural adaptation to gain thermal benefits (Paclík & Weidinger 2007). Nonetheless, we acknowledge that roosts are also located in places relatively safe from predation and that roosts may serve as information centres, although Short-toed Treecreepers are not known to forage socially.

We further test the idea that during the non-breeding season communal roosting is more common than during the breeding season, based on the assumption that thermal benefits associated with communal roosting are minimal during the breeding season. As a result, we hypothesize that numbers of roosting treecreepers correlate more strongly with meteorological factors during the non-breeding season than they do

Figure 1. Locations of roosts in Bergen, Noord-Holland, The Netherlands (dots) and monitoring route (line) used this study. Inset shows location (black dot) of study sites within Western Europe.

during the breeding season. Further, we argue that roost location (i.e. exposure to rain, wind, cold) is determined to a greater extent by weather during the non-breeding season than it is during breeding. Finally, we hypothesize that during the breeding season, roosts are mainly used by non-brooding individual birds, such as single males, because paired birds roost primarily in nesting cavities.

Finally, although we only survey treecreepers roosting on buildings and not on or in trees, the surroundings of roosts may be of importance; we predict that the surroundings of roost locations have more tree cover than random locations to offer increased shelter from inclement weather, foraging possibilities or safe passage from predation to roost locations.

METHODS

Roost sites were identified by visually detecting traces of urea using a flashlight (and in some cases using binoculars) on the gables of residential buildings during 2017. Prior to using flashlights on a building, homeowners were asked for permission. In total, we investigated 127 roost sites on 121 residential buildings during 487 counts performed during a period spanning from 1 January 2018 through 31 December 2020. Because some days counts were performed during both early morning and evening, we only used counts performed during the evening (before midnight), reducing the number of analysed counts to 360. Counts were not restrained to a particular temporal schedule, but rather occurred opportunistically (although independent of weather conditions). All roosts were located within the city limits of Bergen, Noord-Holland, The Netherlands (52.667°N, 4.716°E) along a 13.26-km fixed transect in an area of c. 3 km^2 (Figure 1). Roosts were considered a single roost if located on a single wall, even if birds were loosely associated, because on residential buildings treecreepers are known to roost on average c. 20 cm from other groups of individuals (Glutz von Blotzheim & Bauer 1993). We recorded roost orientation in degrees, 0° representing north and 180° representing south.

Temporal variation in roost use

To explore temporal patterns in roost use through time, we first plotted the number of sites through time with no treecreepers ('vacant roosts'), number of sites with single individuals ('individual roosts') and number of sites that contained multiple individuals ('communal roosts'). Treecreepers are known to breed from March through July in Northwest Europe (Glutz von Blotzheim & Bauer 1993) and our sampling efforts were concentrated during the non-breeding season, when Treecreepers are known to most frequently roost communally. We here define the non-breeding season (n = 353) as running from September through February and the breeding season (n = 135) from March through August. We perform a Wilcoxon rank sum test in R using package 'stats' to compare distributions of vacant, individual and communal roosts between the non-breeding and breeding seasons. We report frequencies of roosting numbers during both the non-breeding and breeding season (Table 1).

Meteorological correlates of roost use

We downloaded detailed meteorological data from www.knmi.nl for IJmuiden, The Netherlands, which is the nearest weather station to the study site and located approximately 25 km from Bergen.

We applied generalized linear models (Nelder & Wedderburn 1972) in R (v. 4.1.2) base packages to determine effects of factors that we deemed may logically affect roost use: daily duration of precipitation, daily sum of precipitation, daily mean wind direction (which we broke down into variables corresponding to the four cardinal directions), daily mean wind speed, daily maximum temperature, daily minimum temperature, daily mean temperature, daily mean humidity and daylength, which we used as a measure to infer patterns dependent on seasonality (e.g. breeding, time for foraging during the non-breeding season). We modelled total daily number of roosting treecreepers over all sites. Because our data represented count data and was overdispersed, we used a quasi-Poisson family

Table 1. Frequencies of numbers of Short-toed Treecreeper at roosts in the non-breeding and breeding seasons.

Number at roost	Non-breeding (Sep–Feb)	Breeding (Mar–Aug)
0	32,959	5363
1	2900	388
2	1484	348
3	527	49
4	237	14
5	113	1
6	46	1
7	2	0
8	2	0

function. We used the 'vif' function of package 'car' (Fox *et al.* 2023) to test for variance inflation and used ANOVAs to detect significant contributions of interaction terms to our model.

We further assessed the effect of wind direction on the spatial selection of roosts by applying a Rayleigh Test of Uniformity (RATU) and Kuiper's one-sample *V* test of uniformity on the circle, both in the R-package 'circular' (Lund *et al.* 2001) to test for significance of patterns of correlation between wind direction and roost orientation. A density plot revealed that all orientations between 0° and 360° are represented in our data set, without major intervals missing. The distribution of orientations of all used roost locations is similar to orientations of all available roost locations (n = 183). A Rayleigh Test of Uniformity is used to detect departures from uniformity in circular data and assumes a unimodal distribution (there is a single cardinal direction which is preferred over all others), whereas Kuiper's *V* assumes a multimodal distribution, where there may be more than one cardinal direction which is chosen more than expected. To interpret the results of both these tests, we also plot roost orientation by prevailing wind direction.

Environmental characteristics of roost location

To quantify environmental correlates of roost location, we drew 25-m and 100-m buffers around the 127 known (and occupied during the study period) roost locations using function 'st_buffer' of package 'sf' (Pebesma 2018, Pebesma & Bivand 2023) in R. Then, we extracted from these buffers underlaying land use characteristics from the Land Use shapefile (Bestand Bodemgebruik 2015) available from www.data.overheid.nl. We calculated mean cover of each dominant land use type (agricultural, urban, recreational, water, traffic, forest) for all buffers.

Although we did not make an explicit effort to locate every roost in the study area, we also quantified land use characteristics of the entire study area by assessing these characteristics in the same buffers surrounding 127 randomly sampled points (using function 'st_sample' of R package 'sf' in the study area, to contrast with characteristics of known roosts. We performed a two-sided t-test in R to test for significant differences in means between land cover variables of roost sites and simulated sites. We report values for 25-m buffers; there were no differences in significance of environmental variables with 100-m buffers, but mean differences between roost locations and 100-m buffers were smaller than between 25-m buffers and roost locations.

RESULTS

Out of 44,640 observations, there were 6318 observations (14.2%) with roosting birds. The mean number of roosting treecreepers per site (excluding null-observations) was 1.62 ± 0.95 (±SD). The maximum recorded number of roosting treecreepers per site was eight (Table 1). The mean total number of roosting Treecreepers at all 127 sites per day was 25.2 ± 10.68. The maximum cumulative number of roosting Treecreepers found on one day at all sites was 55.

Temporal variation in roost use

Vacant roosts always constituted the largest proportion of roost sites (86.8 ± 3.5%), followed by individual roosts (7.6 ± 3.9%) and communal roosts (6.6 ± 3.5%). A Wilcoxon rank sum test revealed that there was a significant difference in the distributions of vacant, individual and communal roosts between the non-breeding and breeding seasons (W = 15195, P < 0.001). Vacant roosts were most common in the breeding season (Figure 2; 89.5 ± 3.8% vs. 85.8 ± 2.9% in winter), individual roosts in the non-breeding season (mainly in fall, 8.0 ± 4.2% vs. 6.7 ± 2.5% in the breeding season) and communal roosts during the non-breeding season (mainly late winter, 7.3 ± 3.4% vs. 4.8 ± 3.3% in the breeding season). The maximum number of consecutive nights of roost occupancy was 99, the mean number of consecutive nights of occupancy year-round was 3.1 ± 2.3 (Figure 3). During the non-breeding season only, the maximum number of

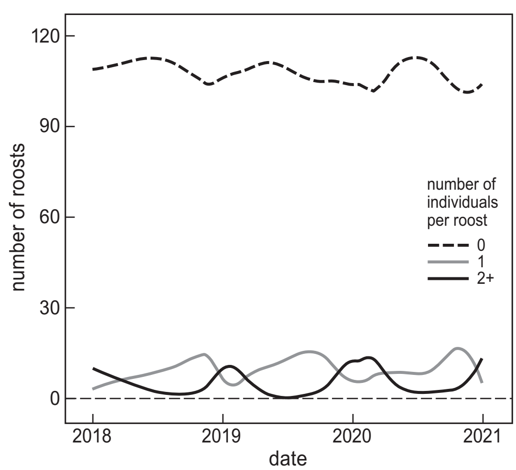

Figure 2. Temporal variation in roost use by Short-toed Treecreeper in Bergen, The Netherlands, showing frequencies of vacant, individual and communal roosts during the study period. Vacant roosts and individual roosts are mostly found during the breeding season, whereas communal roosts are more common during non-breeding.

consecutive nights of roost occupancy was 95, the mean number of consecutive nights of occupancy was 3.4 ± 2.6. For 25% of the largest roosts (measured as mean number of individuals across time), mean occupancy was 5.1 ± 2.9 consecutive nights. This indicates that roosts with large numbers of roosting treecreepers, all from the non-breeding season, were also characterized by the most continuous use, indicating that these roosts likely had the most favourable roosting conditions.

Meteorological correlates of roost use

Of the meteorological variables used to explain numbers of roosting treecreepers, maximum daily temperature was the strongest (negative) predictor of variability in numbers across the entire year, followed by wind speed, daylength, and rainfall (Table 2). During the non-breeding season, wind speed was the strongest negative predictor of numbers, together with minimum daily temperature, daylength and relative humidity, contrasting with the breeding season, when

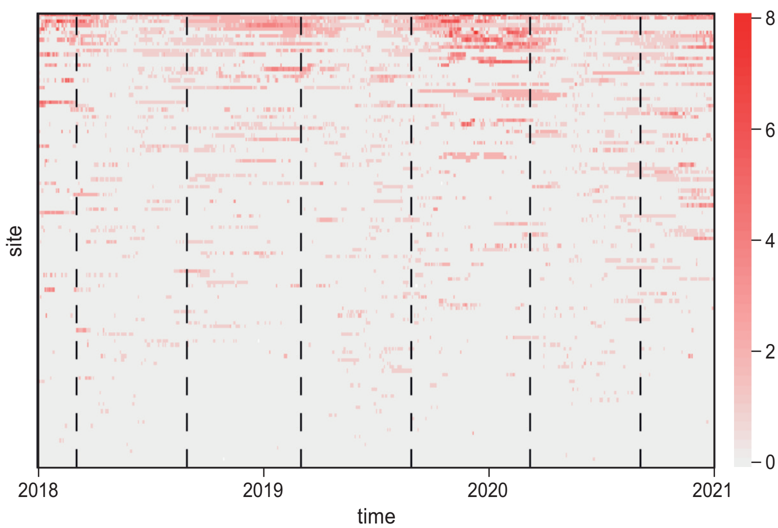

Figure 3. Roost site occupancy and numbers of treecreepers through time. A relatively small number of sites hold the majority of roosting birds and most roosts are used only opportunistically. Note that the breeding season is represented by fewer observations than the non-breeding season. Dashed lines indicate boundaries of breeding and non-breeding seasons.

Table 2. Results of generalized linear models explaining the variability in roost use by Short-toed Treecreepers in Bergen, The Netherlands, in 2018, 2019 and 2020. Only the highest scoring models (with or without interactions) are shown. *$P < 0.05$.

Model parameter	Parameter estimate	SE	t	P
Model: total number of Treecreepers per roost year-round ~ daylength + wind speed + max day temp + precipitation sum				
Daylength (h)	–0.001	0.001	–5.669	<0.001*
Wind speed (m/s ×0.1)	0.003	0.001	4.974	<0.001*
Max. day temp. (°C ×0.1)	–0.003	0.001	–7.092	<0.001*
Precipitation sum (mm ×0.1)	0.001	0.001	2.213	0.028*
Model: total number of Treecreepers per roost in non-breeding season ~ daylength + wind speed + minimum day temp + relative humidity				
Daylength (h)	–0.001	0.001	–4.750	<0.001*
Wind speed (m/s ×0.1)	0.004	0.001	7.055	<0.001*
Min. day temp. (°C ×0.1)	0.003	0.001	–6.462	<0.001*
Relative humidity (%)	0.006	0.003	–2.549	0.011*
Model: total number of Treecreepers per roost in breeding season ~ daylength				
Daylength (h)	–0.004	0.001	–3.597	<0.001*

only daylength significantly correlated with numbers. Other factors and interactions between variables had a non-significant ($P > 0.05$) effect on the number of roosting treecreepers. We removed collinear variables, based on vif-values > 2, from our models.

Roost sites were evenly distributed along the 0–360˚ continuum (Figure 4). As expected in a uniform distribution, roost sites (including roosts frequently vacant) were located at a mean angle of 172.0° ± 115.9° and 25% of the largest roosts were located at an angle of 182.8° ± 122.2°. Orientations of all used roosts were similar to orientations of available roosting sites, indicating that some seemingly suitable roost sites were apparently never used due to unknown reasons. The selection of orientation of used roosts by treecreepers is not independent of wind direction. RATU revealed a non-random selection of orientation ($t = 0.1262$, $P < 0.0001$). Further, Kuiper's V indicated a significant departure from uniformity as well ($P < 0.01$). From the combined results of these tests we can conclude that treecreepers tend to non-randomly select the orientation of roosts, with a single dominant direction involved and perhaps a secondary direction as well. Spatial plotting of roost orientation selection by wind direction (Figure 5) showed that with northerly and easterly winds (most frequently associated with low temperatures during Dutch winters), the difference in orientation between vacant and occupied roosts was greatest.

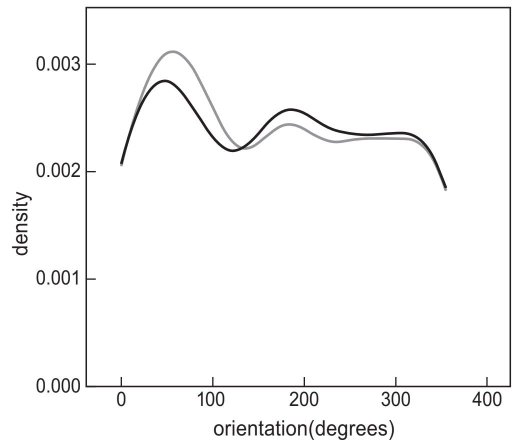

Figure 4. Density distribution of all available roost locations (grey) and used locations (black), indicating that roost orientations are rather evenly distributed along the 0–360°-continuum and that on average the distribution of orientations of used roosts does not differ from the orientation of all available roosts (n = 183).

Environmental characteristics of roost site selection

The surroundings of roost sites (25 m radius) were mainly characterized by traffic infrastructure (78.7%), and to a lesser degree by residential buildings (8.8%), agriculture (9.7%) and forest (1.4%). For the 127 random sites within the study area, these percentages were 74.7%, 8.5%, 14.3% and 1.4% respectively. Means per site of these landscape characteristics did not differ significantly between random and roost sites ($P > 0.05$ for all variables).

DISCUSSION

Temporal variation in roost use

The use of communal roosts by treecreepers was mainly centred in the late winter and communal roost use decreased steeply after late winter to near-zero midsummer. Breeding activity from March onwards also coincided with a decrease in the use of communal roosts, but if communal roost use were not dependent upon meteorological circumstances, an increase in communal roost use may be expected after juveniles fledge in summer. We cannot rule out the possibility that family groups roost elsewhere, e.g. in crevices in large trees, as the species is known to do (Glutz von Blotzheim & Bauer 1993) during non-breeding.

The influence of weather on roost use

We found a negative correlation between several meteorological characteristics that may be associated with survival: daylength, maximum temperature, wind speed and relative humidity. The influence of both daylength and weather on the number of roosting birds was particularly noticeable during the non-breeding season, whereas during the breeding season only daylength was negatively correlated, probably as a result of decreasing numbers in the roost towards midsummer. The exact peak of communal roost use seems to vary slightly between years: in the winter of 2017–2018 peak use was in early January 2018 (but no data for December 2017), in 2019 it was in early January, in 2020 in January and February (February of 2020 was particularly cold and snowy and coincided with frequent communal roosting) and likely peaked in early 2022 (no data).

Wind direction appears to influence the selection of roosts: northern and eastern winds, which during the winter in The Netherlands are generally associated with relatively cold and dry weather, drive birds to use roosts with a more southern or western exposure. Although Rankin & Rankin (1939) observed that Eurasian Treecreepers chose roosts on the side of tree

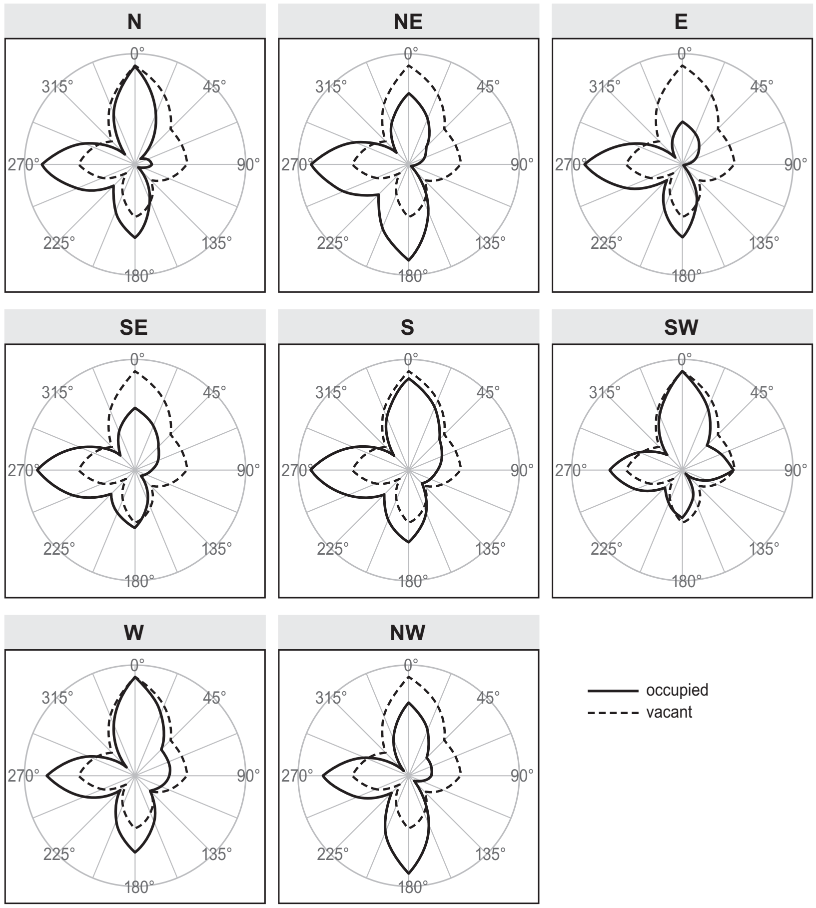

Figure 5. Selection of roost orientation by Short-toed Treecreeper under different wind directions. The difference between orientation of occupied vs. vacant roosts is greatest with winds coming from a northern or eastern direction.

trunks not exposed to wind, they only did so if windy weather was accompanied by humid or rainy conditions. Our results similarly indicate that during the non-breeding season, the combined forces of wind speed and humidity and low temperatures are sufficient to influence the number of roosting treecreepers. Although we do not have data on treecreepers roosting in natural roosts (e.g. tree crevices and cavities), we propose that roosts on buildings offer thermal benefits that rival those of natural roosts rather than reflect a lack of natural roost opportunities, because numbers in our study fluctuate strongly and a large proportion of treecreepers are not accounted for during certain days on urban roosts.

Characteristics of roost environment

Most roosts were, unsurprisingly, located in an environment having large components of urbanization and road infrastructure. Suitable roost locations are not in reality randomly dispersed across the landscape; we presume that roosts of treecreepers are restricted to human-made structures and crevices in (larger) trees, as they are not known to roost on the ground or perched (Glutz von Blotzheim & Bauer 1993). We did not search for treecreepers roosting in or on trees and so our spatial sample is biased towards an anthropogenic environment. Nonetheless, environmental conditions at randomized sites did not differ significantly from those surrounding roost locations, revealing that roost locations are likely not selected based on their surroundings, but more likely on the characteristics of the roost itself. However, it is possible that our environmental data is not fine-grained enough or is missing variables that are relevant to treecreepers.

Passerine roosting behaviour: filling in knowledge gaps

Our study points towards an important role for roosts as thermal refuges for passerines during the non-breeding season and shows that most roosts are used only incidentally, with a few apparently optimal roosts used most frequently and consistently. Roosting behaviour is particularly poorly studied in tropical passerines and thermal benefits should be relatively less important in this group compared to their temperate counterparts, but this hypothesis remains untested as far as we know. The suitability of roosts should be quantified further, particularly in terms of microclimatic conditions, influence of substrate and potential sources of roost disturbance such as predation potential and disturbance by anthropogenic activities. Also, we know little of daily movements of passerines to and from their roost locations and the influence of the proximity of suitable foraging habitat on roost choice. We hope our work sets the stage to further answer some of these questions in the future.

Roosts as thermal refuges: conservation implications

Our study demonstrates that particularly during the short days of the non-breeding season, treecreepers prefer roost sites that are not exposed to cold winds. Further, use of (communal) roosts increases with increased relative humidity and with lower temperatures. Treecreepers naturally roost within the bark of large trees, but it is apparent that in an urban setting, large numbers make use of buildings for roosting. Although we did not search for roosts on natural substrates, large fluctuations in the numbers of roosting treecreepers on buildings hint at the fact that trees are used for roosting during more meteorologically benign conditions. Short-toed Treecreepers, at least in The Netherlands, are more common in forested habitats than in urban habitats or even urban habitats with a large green component during the non-breeding season (Sovon 2024), indicating that the presence of buildings suitable for roosting alone is not sufficient to increase populations of treecreepers. Although it is possible that trees offer suboptimal roosting conditions during inclement weather, it is likely that large trees with rough bark and crevices provide much better shelter for roosting treecreepers than do young trees or trees with smooth bark, and that buildings, where present, are merely used opportunistically. The presence of old, large trees likely remains a requirement for maintaining healthy treecreeper (and other bark-probing bird) populations. However, in urban environments, where treecreepers benefit by the presence of buildings suitable for roosting, a combination of these buildings and mature trees for both roosting and foraging is optimal.

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SAMENVATTING

Hoewel bekend is dat boomkruipers *Certhia* spp. gemeenschappelijk slapen, zijn de factoren die verband houden met het gebruik van slaapplaatsen nooit gekwantificeerd. Hier onderzoeken we de invloed van omgevingsvariabelen op het slaapgedrag van de Boomkruiper *C. brachydactyla* in een stedelijke omgeving in Nederland. We voerden nachtelijke transecttellingen uit van 120 slaapplaatsen op 487 dagen gedurende een periode van drie jaar. We hebben het totaal aantal vogels per verblijfplaats per dag in verband gebracht met meerdere relevante omgevingsfactoren. Zowel het gemiddelde als het maximale aantal boomkruipers waren positief geassocieerd met lage minimumtemperaturen en noordenwind en negatief met een hoge maximale dagtemperatuur en met de daglengte. Uit ons onderzoek blijkt dat Boomkruipers reageren op temperatuurschommelingen op de korte termijn door hun ruststrategie te veranderen. Het gemeenschappelijk slapen van de soort is dus waarschijnlijk vooral een gedragsmatige reactie op een combinatie van weersomstandigheden en de daglengte. De meeste slaapplaatsen zijn over het algemeen leeg of herbergen een klein aantal boomkruipers, en een paar ogenschijnlijk optimale locaties herbergen consistent grote aantallen. Lege slaapplaatsen pieken in aantal tijdens het broedseizoen (89,5±3,8% versus 85,8±2,9% in de winter), terwijl slaapplaatsen van losse vogels (8,0±4,2% versus 6,7±2,5% in het broedseizoen) en gemeenschappelijke slaapplaatsen (7,3±3.4% versus 4,8±3,3% in het broedseizoen) het meest voorkomen in de winter. Ons onderzoek vult een belangrijke leemte in onze kennis over het slaapgedrag van zangvogels op, maar er valt nog veel te leren.

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