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Research

Secrets of the night: roost sites and sleep disturbance factors during the autumn migration of first-year white stork *Ciconia ciconia*

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The migration phase of birds is divided into two main states: stopovers and actual migratory flights. For soaring birds, such as storks, nighttime is especially important to conserve energy and to start the next day in favourable weather conditions. Although there is a large number of recent studies on white stork *Ciconia ciconia*, for example using advanced technologies such as GPS technology, the nocturnal behaviour of the species is still an enigma. Thus, we GSM–GPS-tagged 90 immature storks and checked their nocturnal behaviour, especially roost disturbance, during their first autumn migration from breeding grounds in southern Poland to wintering places in Africa. Storks roosted on three types of site: on buildings, on the ground or in trees. Birds that roosted on the ground had a higher probability of nighttime disturbance than those that used trees or buildings. The probability of disturbance at night was also related to longitude and latitude; the most easterly birds and those at the start of the migration route were disturbed more often during the night. Furthermore, and interestingly, environmental conditions at roosts were also significantly related to the probability of disturbance; birds roosting at tree sites with higher NDVI (greener) and with higher levels of artificial light both had a lower probability of disturbance. A possible explanation of this could be related to lower potential predatory pressure at night. We found that after long flights birds were disturbed more often at night, and that disturbed birds migrated further the next day. For a better understanding of the nocturnal behaviour of storks, as well as of other migratory birds, the use of modern technological tools with greater precision is recommended.

Keywords: disturbance, light, migration, NDVI, night, white stork

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Introduction

The migration of birds has fascinated people for millennia (Berthold 2001) and many migratory strategies have developed on an evolutionary timescale. For continuing their migration, birds must accumulate energy at stopover sites, but also survive roosting (Schmaljohann 2022). For large soaring birds, such as raptors and storks, migration is only possible during favourable weather conditions, typically sunny days with sufficient wind (Eisaguirre et al. 2019). Birds often have to wait in secure locations, sometimes referred to as stopover sites, until conditions are favourable to continue on their migration. For instance, unfavourable atmospheric conditions can halt their migration. One such species is the white stork *Ciconia ciconia*, a large soaring migratory bird, which pauses during migration when thermal conditions are weak, especially during the mornings and evenings (Berthold 2001, Shamoun-Baranes et al. 2003, Becciu et al. 2020, Siekiera et al. 2021). Due to modern technology our knowledge of bird migration has increased rapidly in recent years, with the white stork being a classic subject of avian migratory studies (Flack et al. 2016, Siekiera et al. 2021). However, while published results on migratory patterns and decisions focus on diurnal activity, behaviour at night remains much of a mystery. Surviving the night in a good condition is crucial to continuing migration (Lack 1968).

White storks sleep either on the ground or on elevated places, they either pull back their head with the beak still pointing forwards and downwards or simply tuck their head into their neck feathers (Bocheński and Jerzak 2006). As in many other birds, sleep is sensitive and modified by internal and external factors. Recently there has been increasing evidence that artificial light on migratory routes negatively influences sleep patterns (Russart and Nelson 2018), however paradoxically there is much less known on whether spatial variation in nighttime light pollution, or distance travelled, affect sleeping behaviour.

Here we study GSM–GPS-tagged immature, first-year white storks, about to embark on their first challenging migration to wintering places in Africa (Rotics et al. 2016). The aims of this paper are to describe sites where white storks roost, to determine how often roosting was disturbed, and to investigate the influence of environmental factors (NDVI, artificial light), geographical position (longitude, latitude) and characteristics of the flight (distance travelled before roosting) on nighttime disturbance. Furthermore, we checked the distance of night movement where it occurred and its influence on the next day's migration travel and survival.

Material and methods

Between 2012 and 2017 a total of 90 white storks (2012: 1; 2013: 5; 2014: 9; 2015: 36; 2016: 37; 2017: 2) were tagged 1–2 weeks before fledging at nests in the Opole voivodeship (district), southern Poland, i.e. at the beginning of their migration route (Fig. 1) and equipped with 27 g, solar GSM–GPS–ACC loggers (DUCK-3 GSM and since 2016 type SAKER-H from Ecotone producer) attached as a backpack through a teflon–nylon harness. Total backpack weight (i.e. transmitter plus harness) was below 3% mean body mass. The transmitters recorded GPS fixes every 30 min. During the first years, because of technological limitations (fast battery discharge), the GPS fixes were set to 60 min intervals. Data were stored on-board until birds were in range of a GSM tower and then the data were transmitted automatically (Rotics et al. 2016, Ossi et al. 2019).

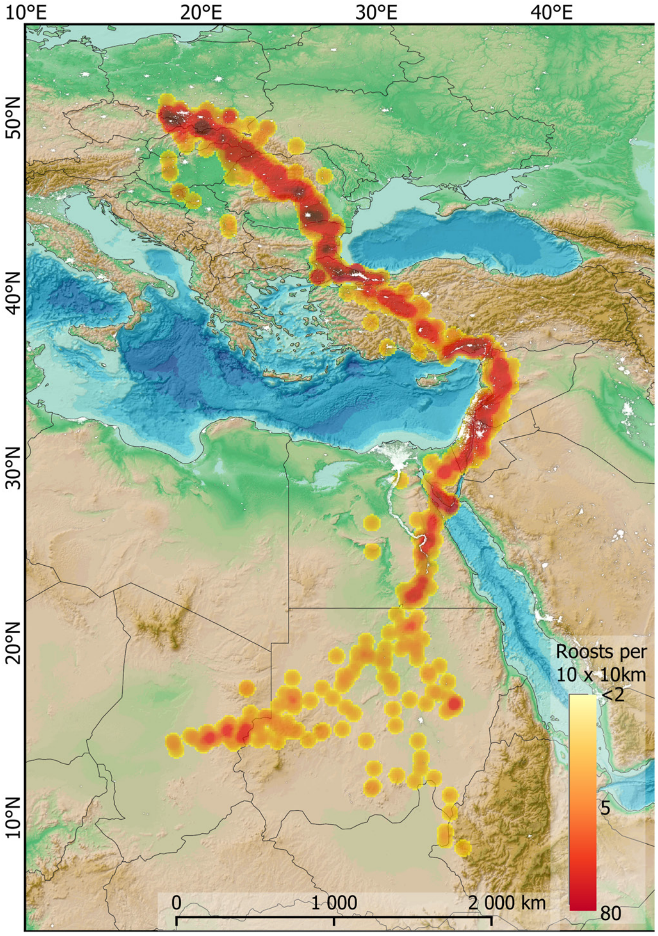

Figure 1. Locations of roost sites during the migration of tagged juvenile white storks *Ciconia ciconia* (imagery reproduced from the GEBCO_2021 Grid) (GEBCO Compilation Group 2021). Roost density was estimated by spatial kernel density interpolation. White patches indicate cities and their intensity of artificial light (Román et al. 2018).

Roost sites

The start of migration was determined when the GPS position was recorded further than 50 km from the natal nest in the direction of migration (Kaatz 2004). Analogically, the end of migration was determined when roost sites, on consecutive nights, were not further than 50 km apart.

Night/roost time was identified as the time between sunset and sunrise in local time. White stork is normally active only during daylight, especially during migration, and this is a rather conservative assumption, because storks come to communal roosting places normally before sunset and stay until the early morning hours (Kaatz 2004, Antczak and Dolata 2006).

The location of the roost site was obtained as an estimated point where the maximum number of GPS fixes (cloud of points showing GPS fixes of a sleeping bird) were at a distance less than 30 m. The accuracy of the GPS–GSM tag is up to 30 m, but has much better accuracy (5 m) in good weather (Ecotone product materials). Next, we manually identified the type of roost site from GPS positions overlaid on Google Earth. Google Earth maps can be zoomed to a scale of ca 1:1000 and even to 1:500. At such scales, it was possible to visually identify the sleeping place/object on which the bird was roosting from the estimated point and cloud of points of successive readings of the sleeping bird. We classified the roosting sites as building (n = 256 cases), ground (n = 531) or tree (n = 621). In the last category we also included the small number of cases (n = 27) roosting on electricity pylons or streetlamps. If a bird stayed in the same roost site the following night we included it as a separate record.

Nighttime disturbance

Our first aim was to analyse nighttime disturbance. Overnight disturbance was established as movement of a bird indicated by GPS data and is assumed to be a measure of sleep discomfort in birds, linked to vigilance and movement (Beauchamp et al. 2003, Lima et al. 2005). To assess it we calculated the distance between the coordinates of successive readings during the night. If the distances between successive locations were at least 40 m, which is more than the theoretical measurement accuracy, it was assigned as a changed location during the night. We excluded nighttime disturbances where we only had a single GPS fix movement greater than 40 m. The assignment of moved/disturbed category was thus always based on more than one GPS fix. In the situation where a bird was disturbed but returned to the same roost, it was still recorded as a disturbance.

We wanted to test whether different types of roosting site (three categories: building, ground or tree) affected nighttime disturbance – we hypothesised that disturbance should be more frequent on the ground because of the possible danger of predation.

To test whether vegetation around the roost influenced disturbance we included normalized difference vegetation index (NDVI) in our analysis. NDVI indicates the amount of chlorophyll in vegetation (Pettorelli et al. 2005) on a scale from 0 to 1; higher values indicate a greener location, while values close to zero indicate no vegetation. We hypothesised that disturbance should be less frequent in greener locations because of possibility to roost safer or to watching effectively potential predators. For the NDVI variable we took the mean value of all pixels within a 750 m radius of the roosts using the zonal statistics algorithm in QGIS. NDVI maps (Didan 2021) were downloaded from the NASA earth data repository (NASA 2019) for the period from 1 Aug 2016 to 20 Sep 2016. We chose this year because 41% of birds were tagged in 2016, and as indicative of greenness in other years. The satellite images (from MODIS aboard NASA's Terra satellite) are biweekly images of NDVI or EVI (Landsat Enhanced Vegetation Index) with 250 m resolution.

Roost types differ markedly in their NDVI. A linear model revealed significant differences in NDVI between roost types ($df = 2$, $F = 448.59$, $p < 0.001$). The predicted mean value of NDVI for buildings was 0.63 ± 0.012 SE, for trees was 0.51 ± 0.009 SE and for ground was 0.22 ± 0.009 SE (Supporting information; Tukey tests for each comparison were significant at $p < 0.001$). To control for this relation in the disturbance occurrence model we included an interaction term: roost site × NDVI.

Artificial light could affect sleep, so the birds sleeping at sites with higher light pollution should be disturbed more often. On the other hand, the higher light pollution probably increases the chance of seeing potential predator and such place could be safer. For the light intensity variable we took the mean value of all pixels within a 750 m radius of the roosts using the zonal statistics algorithm in QGIS. We used night light measurement as the value of the grey scale of pixels around roosting sites. A night light image with 500 m resolution per pixel and sensor resolution 750 m (SNPP-VIIRS Nighttime Light Dataset) (Román et al. 2018) was obtained from NASA's Global Imagery Browse Services (GIBS), part of NASA's Earth Observing System Data and Information System (EOSDIS) and was available only as a single snapshot in time for 2012 and 2016.

We were also interested in whether the probability of night disturbance varied between the start, middle and end of migration, so we added longitude and latitude as explanatory variables. However, the probability of disturbance might be related not to the geographic position but to the day of migration which was added as a covariate.

We hypothesised that longer flight distance before roosting would increase the probability of disturbance, to test it we used flight distance before roosting as an explanatory variable. It was estimated as the distance between two consecutive roost sites (from previous to current roost; almost each night the roost sites were different – only 3.7% were at the same place).

We found a positive correlation (0.73) between latitude and NDVI and a negative correlation between longitude and NDVI (−0.74) (both significant at $p < 0.001$; for all correlations see Supporting information). However, all variance inflation factors (VIF) were below 3.6 (Supporting information); and all variables could be included in models without concerns for multicollinearity (James et al. 2013).

For the disturbance occurrence analysis we used a generalised linear mixed model with a binomial distribution (M1). We included roost site, NDVI, roost site × NDVI, light intensity, longitude, latitude, day number of the migration and flight distance as explanatory terms. In this dataset we had repeated measurements of individual birds on consecutive days of migration, so we added bird id as a random term nested within day number (R syntax: ~ … + *day* + *(1 + day | id)*) to account for the variability in behaviour of different individuals during migration.

Distance of flight after disturbance

For those birds that were disturbed we wanted to test the predictors on disturbance distance. We performed a linear mixed model (M2) based on a normal error structure with bird id as a random effect within day number as for M1. The same explanatory terms as for M1 were used.

Daily distance after roosting and survival

We estimated migration distance after roosting as the distance between two consecutive roost sites (distance from current to subsequent roost). We hypothesised that nighttime disturbance would hinder the ability to fly further. We also wanted to test whether roost type, latitude, longitude and day of migration could affect this distance. In this analysis we used a linear mixed model (M3) based on a normal error structure with bird id as a random effect within day number as for M1.

Lastly we wanted to assess whether death during migration was affected by disturbance the day before. Death was indentified when the position of the logger was the same for successive days until battery discharge (we excluded from the analysis any potential logger issues). We used a generalised linear mixed model with a binomial distribution (M4) and random effects as in M1. Nightime disturbance (y/n) and day number were included as explanatory variables.

Software

Analysis was performed in R software ver. 4.1.1 (<www.r-project.org>) using lme4 (Bates et al. 2015), ggplot2 (Wickham 2016), emmeans (Lenth 2020) and ggeffects (Lüdecke 2018) packages. We tested the significance of explanatory variables using likelihood ratio tests (LRT) or F tests provided by the function ‘drop1’ which compares the full model to a reduced model where the target variable had been dropped, based on Akaike information criterion (AIC). Post-hoc comparisons were done using Tukey tests. All GIS analyses were performed using QGIS (QGIS 2020).

Results

We recorded 1408 roosting sites (Fig. 1). The mean number of days with working GPS transmitters per bird was 15.6 ± 9.5 SD (min = 1, max = 45). Of 90 tagged storks, 41 finally arrived at their migration destination in Africa, and the rest died on migration; 8 during nighttime (8.9% of all tagged birds), mainly from unknown causes

Nighttime disturbance

A total of 415 night disturbances were recorded. The model (M1) parameters of nighttime disturbance are shown in Table 1. There was a significant relationship of disturbance with longitude (LRT = 11.721, df = 1, p = 0.001) and latitude (LRT = 6.256, df = 1, p = 0.012). Birds in the most easterly roosts (Fig. 2A) and in the north at the start of migration (Fig. 2B) were disturbed more often during the night. The interaction roost site × NDVI was significant (LRT = 13.640, df = 2, p = 0.001, Fig. 2C). The interaction between roosting site and mean NDVI indicates that there was a decrease of night disturbance in areas of higher NDVI only for roost sites in trees – in greener areas the probability of night disturbance was lower (Fig. 2C). In a model without the interaction the main effect of roosting site was significant (LRT = 70.374, df = 2, $p < 0.001$). The predicted probability of nighttime disturbance was highest for birds roosting on the ground (0.446 ± 0.030) and was significantly different from that for birds roosting on buildings (0.118 ± 0.025) and in trees (0.190 ± 0.018; Tukey post-hoc tests; both $p < 0.001$). The difference between the probability of disturbance in trees and on buildings was not significant (p = 0.076). The flight distance before roosting was also significant (LRT = 9.833, df = 1, p = 0.002); after flying long distances birds were disturbed more often (Fig. 2D). Finally, light intensity was also significant (LRT = 6.087, df = 1, p = 0.014); higher levels of light were associated with lower probability of disturbance (Fig. 2E).

Distance of flight after disturbance

The mean distance of nocturnal travel (night flight after disturbance) was 2.16 km (min = 0.1 km; max 16.3 km; SD = 2.32). The model (M2) parameters of distance of flight after disturbance are shown in Table 1. The roost site × NDVI interaction was significant (F = 5.837, df = 2, p = 0.003). There was a decrease of night movement distance in areas of higher NDVI values only for roost sites in trees – in greener areas the distance was smaller (Fig. 2F). Flight distance (F = 0.093, df = 1, p = 0.761), light intensity (F = 2.564, df = 1, p = 0.110), latitude (F = 0.288, df = 1, p = 0.592) and longitude (F = 2.393 df = 1, p = 0.123) were not significant.

Daily distance after roosting and survival

The model (M3) parameters of the daily distance after roosting are presented in Table 1. We found that night disturbance affected the mean distance moved in the following day; it was significantly longer for birds disturbed the previous night (134 km ± 18.0 SE) compared to the birds that were not disturbed (106 km ± 13.10 SE, F = 9.646, df = 1, p = 0.002). There was also a significant relationship with longitude (F = 19.775, df = 1, p = 0.001); birds in the more easterly roosts travelled longer distance daily.

We recorded 30 deaths and 962 non-deaths after roosting without disturbance and 11 deaths and 405 non-deaths after roosting with disturbance. The model (M4) parameters of the probability of death are presented in Table 1. We found no effect of night disturbance on the probability of death (LRT = 0.031, df = 1, p = 0.859).

Table 1. Results of four mixed models (binomial models – M1, M4, linear models – M2, M3). Please note that the model parameters were tested by t- or z-statistics and tests of the main effects are presented in the main text.

	Estimate	SE	t or z	p
M1: Nighttime disturbance, n = 1408				
(Intercept)	−3.163	0.758	−4.172	< 0.001
Light	−0.004	0.002	−2.384	0.017
Flight distance	0.00186	0.00059	3.171	0.002
Type: tree	−0.356	0.284	−1.251	0.211
Type: building	−2.284	1.060	−2.156	0.031
NDVI	0.561	0.683	0.822	0.411
Latitude	0.029	0.012	2.404	0.016
Longitude	0.060	0.018	3.424	0.001
Day	−0.003	0.008	−0.329	0.742
Type: tree × NDVI	−2.513	0.702	−3.581	< 0.001
Type: building × NDVI	0.077	1.676	0.046	0.964
r(ID) = 0.0004 ± 0.0191 SD; r(Day) = 0.0001 ± 0.0078 SD				
M2: Distance of flight after disturbance, n = 414				
(Intercept)	0.475	1.294	0.367	0.714
Light	−0.004	0.003	−1.601	0.110
Flight distance	0.00032	0.00106	0.305	0.761
Type: tree	1.268	0.504	2.515	0.012
Type: building	−2.330	2.319	−1.004	0.316
NDVI	1.323	1.059	1.250	0.212
Latitude	0.010	0.019	0.536	0.592
Longitude	0.046	0.030	1.547	0.123
Day	−0.011	0.016	−0.661	0.527
Type: tree × NDVI	−4.428	1.240	−3.570	< 0.001
Type: building × NDVI	1.494	3.651	0.409	0.683
r(id) = 0.2823 ± 0.5313 SD; r(Day) = 0.0007 ± 0.0272 SD				
M3: Daily distance after roosting, n = 1318				
(Intercept)	3.296	0.580	5.683	< 0.001
Nighttime_disturbance: yes	0.238	0.077	3.106	0.002
Type: tree	−0.044	0.087	−0.501	0.616
Type: building	0.072	0.125	0.575	0.565
Latitude	0.005	0.010	0.507	0.613
Longitude	0.036	0.009	4.049	< 0.001
Day	0.012	0.016	0.761	0.449
r(ID) = 1.299 ± 1.140 SD; r(Day) = 0.005 ± 0.069 SD				
M4: Survival, n = 1408				
(Intercept)	−3.879	0.378	−10.252	< 0.001
Nighttime_disturbance: yes	0.042	0.382	0.111	0.911
Day	0.007	0.014	0.535	0.592
r(ID) = 2.3006 ± 1.5168 SD; r(Day) = 0.0005 ± 0.0229 SD				

r(id) – repetitive random effect of id; r(Day) – repetitive random effect of day; SE – standard error; SD – standard deviation.

Discussion

Using data from GSM–GPS-tagged birds we show that the first autumn migration can be very challenging for white storks, a soaring bird species. As previously reported, not all birds reached wintering grounds in Africa (Flack et al. 2016, 2018, Rotics et al. 2016). However, we now show that nighttime roosts play an important role during migration. Bird species whose migration depends on thermal currents, such as white storks, must rest overnight. White storks refuel both before and after their overnight rest (Kaatz 2004, Siekiera 2021), and need to conserve energy before starting a long flight of up to 600 km and optimise their timing of migration (Alerstam 2009). Overnight disturbance of sleeping birds, here detected using GSM–GPS tags, can be energetically costly, or in the case of birds sleeping on the roofs of buildings even a few steps may increase the risk of injuries and birds have developed the ability to sleep with one eye open (Amlaner and Ball 1983, Rattenborg et al. 1999) to increase vigilance.

We show that immature storks are more disturbed at night at higher latitudes close to their natal sites and at more easterly longitudes. We hypothesised that young storks sleep in more relaxed conditions there, because of fewer predators than in Africa. However, knowledge on these aspects of avian ecology in general, and white stork in particular, is very limited and needs further study in the future. Lima et al. (2005) mentioned that potential predation is the most important factor influencing roost choice and disturbance. This is especially apparent in the differences in disturbance rates experienced by storks roosting on the ground and those on structures (trees, buildings) above. Storks roosting on the ground were

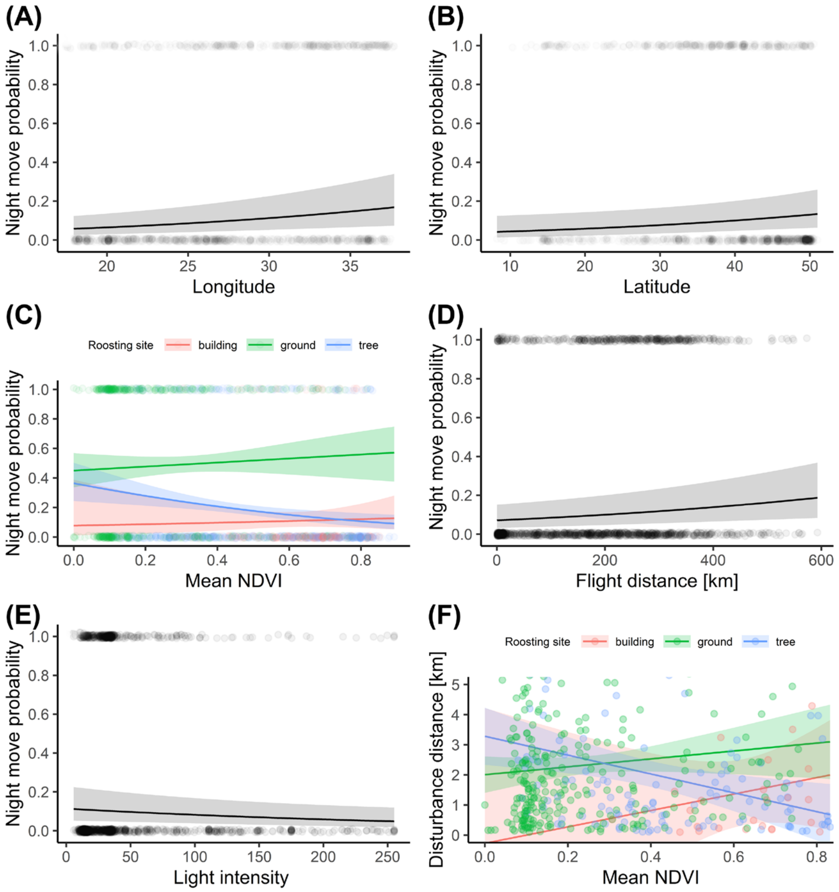

Figure 2. Significant predictions (solid lines) of two different mixed models (shaded area indicates 95% confidence interval). (A)–(E) Binomial model (M1) of nighttime disturbance/movement probability. (F) Linear model of distance after night disturbance. Circles represent observed data, jittered around 0 or 1 in(A)–(E).

recorded in Europe and the Middle East, but especially in Africa, where predation of white stork by large carnivores has been reported (Kruuk and Turner 1967, Temu et al. 2018). NDVI is linked to the presence of trees (Pettorelli et al. 2005) that offer a safe roost but which may also be more productive habitats for foraging. In the case of roosting sites in trees in areas of higher NDVI they were disturbed less during the night in contrast to areas of lower NDVI where the opposite trend was observed. We think this is also related to predation, in more complex green areas there is a lower risk of predation. Further analysis of movement during the night revealed that birds in areas of low NDVI (presumably fewer trees) move longer distances during the night after disturbance in order to search for safer roosting. Surprisingly, light pollution, previously indicated as a danger for migratory birds and other animals via disrupted sleep (Raap et al. 2015, Cabrera-Cruz et al. 2018), had a rather positive effect on storks i.e. lower levels of disturbance. Storks spend nights on building roofs in villages, thus close to street lights (which are visible as light pollution), which may be an anti-predation adaptation. Moreover, disturbed storks in the breeding season may occasionally forage at night, under street-lamps looking for some food sources (Jerzak et al. 2006), which means that occasionally storks may collect food at night, which was also suggested for post-breeding migration by Kaatz (2004). Birds that flew further before roosting experienced more nighttime disturbance. This may be linked to some level of tiredness that negatively affects deep sleep (Bringmann 2018), also in migratory birds (Berthold 2001, Yadav et al. 2021). This indicates that daily migration has an influence on roosting and probably vice-versa (Berthold 2001, Kaatz 2004, Alerstam 2009). According to predictions, storks with disturbed sleep during the night had longer flight distances the next day. This can be linked to the quality of individual storks, affecting both vigilance pattern and energy saving to continuing migration (Sirot 2006).

Finding safe roosting places is important for the continued migration by storks, and probably also for other soaring birds that undertake daily movements (Alerstam 2009). However, roosting of migratory birds remains more secretive than daily movements, when visible information can be linked mainly to data from GPS-tags (Flack et al. 2016, 2018). Our study has some limitations: 1) storks in communal roosts could move (e.g. to a neighbouring tree) due to social interactions rather than external disturbance; 2) only juveniles were tracked; 3) some low accuracy level of the obtained GPS position. However, the criteria for disturbance used (e.g. 30 m) could be used to simply distinguish between true disturbance and movement due to social interactions, but finer resolution GPS should be used, which is now possible due to the fast development in this technology (Nathan et al. 2022). In the future if a whole single roosting flock of storks are GPS-tagged then the research focus could shift to nighttime disturbance of adult birds and pay more attention to the social aspects of communal roosting (Beauchamp et al. 2003).

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Author contributions

Joachim Siekiera: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Validation (equal). **Łukasz Jankowiak**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (lead); Validation (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Piotr Profus**: Conceptualization (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Tim Sparks**: Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Piotr Tryjanowski**: Conceptualization (equal); Investigation (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5x69p8d6m> (Siekiera et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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