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Light data from geolocation reveal patterns of nest visit frequency and suitable conditions for efficient nest site monitoring in Common Swifts *Apus apus*

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ABSTRACT

Capsule: We developed a protocol for efficient monitoring of potential Common Swift *Apus apus* nest sites which considers variation in nest visit frequency across the breeding season and in relation to time of day and weather.

Aims: To investigate patterns of nest visit frequency in Common Swifts in order to improve the efficiency and reliability of the monitoring of nest sites threatened by building renovations.

Methods: We derived information on nest attendance from light data recorded by geolocators from ten adult Common Swifts during three breeding seasons ($n = 686$ individual sampling days) and analysed how nest visit frequency varied across the breeding season and in relation to time of day and weather.

Results: The mean nest visit frequency was 5.63 visits per bird per day (0.32 visits per hour of daylight). The daily number of visits was highest at the beginning of July during chick-rearing. Moreover, it was positively correlated with temperature and negatively correlated with rainfall and wind speed. Nest visit frequency showed a distinct peak around sunset, while also being relatively high in the morning and around noon.

Conclusion: We recommend monitoring potential Common Swift nest sites in Central Europe between the end of June and mid-July during good weather between 0.50 and 7.75 h after sunrise or between 3.00 h before sunset and sunset, when observation bouts of 0.5–2.0 h provide an encounter probability greater than 90%. Our study shows that repurposing geolocator light data – usually used to study bird migration – for investigating nest attendance in cavity-breeding birds can provide important information for bird conservation.

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Breeding birds visit their nest sites for nest building, incubation of eggs, brooding and provisioning of chicks. Therefore, nest visits represent an essential part of the breeding behaviour of birds. Being easy to measure, nest visits have extensively been used for investigating various ecological, evolutionary and behavioural aspects of parental investment (Whittingham *et al.* 1994, Wright & Dingemanse 1999, Barba *et al.* 2009). However, observing nest visits also plays a role in bird conservation, as it may help to identify and monitor nest sites of threatened species, especially in cavity-breeding birds whose nests are often neither accessible nor directly visible from a distance.

Nest visit frequency varies widely between species, ranging between more than ten visits per hour in most songbirds (Whittingham *et al.* 1994, Barba *et al.* 2009) and less than one visit per day in some seabirds (Quillfeldt *et al.* 2007; both during chick-rearing). Moreover, nest visit frequency commonly changes during the course of the breeding season (Lack & Lack 1951, Barba *et al.* 2009) and varies according to the time of day (Stienen *et al.* 2000, Freitag *et al.* 2001) and weather conditions (Lack & Owen 1955). Detailed knowledge on how these factors affect nest visit frequency is crucial for performing nest site monitoring in a reliable and time-efficient way, especially in species with low overall nest visit frequency.

Common Swifts *Apus apus* (hereafter termed Swifts) mainly nest in cavities in buildings over most of their Palaearctic breeding range (Cramp 1985). Population declines observed in several European countries (BirdLife International 2017; for example −53% between 1995 and 2016 in the UK; Harris *et al.* 2018) are thought to be partly linked to modern building techniques which decrease the availability of suitable nest sites for Swifts and other building-nesting birds (Gory 1997, Bauer *et al.*

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2005, Crowe *et al.* 2010, Massa & Borg 2018). For example, when older buildings are renovated and thermally insulated to reduce energy consumption, accessible holes or crevices at the buildings' facades normally vanish, which has been shown to lead to local population declines in Swifts (Braun 1999).

In some countries (e.g. Germany), Swift nest sites are protected by nature conservation laws and must be preserved during renovation works and/or replaced by compensatory measures (nest-boxes; Schaub *et al.* 2016). Owing to the inaccessibility of Swift nest sites, these normally need to be identified by watching the building's facade from the ground. However, due to the generally low nest visit frequency in Swifts (Lack & Owen 1955, Arens 2011a), this is relatively time-consuming and bears a considerable risk of overlooking occupied nest sites. At the same time, although reliable identification of nest sites is a prerequisite for effective conservation measures, existing recommendations for performing field observations at potential Swift nest sites are rather unspecific (Andretzke *et al.* 2005, Ferguson-Lees *et al.* 2011, Rijksdienst voor Ondernemend Nederland 2014). Notably, the guidelines lack a well-founded statement on how long an observation bout at a potential nest site has to last in order to achieve a sufficient probability of observing nest visits in case the nest site is occupied. As this compromises the efficiency and reliability of the monitoring of Swift nest sites, there is a need for a more specific monitoring protocol.

In general, nest attendance in birds can be measured using a variety of techniques such as direct field observations (Whittingham *et al.* 1994), mechanical counters (Barba *et al.* 2009), or transponder-antenna systems (Arens 2011a). Another method is light-level geolocation, i.e. fitting birds with archival tags which record ambient light levels. Primarily, these loggers have been used to track migration routes of small-sized birds (Phillips *et al.* 2004, Stutchbury *et al.* 2009, Wellbrock *et al.* 2017). However, provided that the measurement interval is sufficiently short, the light data from geolocators also allow determining when birds enter or exit a dark cavity and hence offer an opportunity to investigate nest attendance in cavity breeders. So far, this approach has only been applied in a few studies (Guilford *et al.* 2012, Lemke 2014).

In the present study, we investigated the variation of nest visit frequency in Swifts across the breeding season and in relation to time of day and weather conditions using data from light-level geolocators. Based on these data, we developed a protocol for efficient monitoring of potential Swift nest sites with recommendations about how long field observations need to last under different conditions in order to achieve a sufficient encounter probability. With this monitoring protocol, we aim to improve the efficiency and reliability of Swift nest site monitoring prior to building renovation activities as well as monitoring of the efficacy of compensatory measures. In general, we want to promote the supplementary potential of geolocator data for investigating nest attendance in cavity-breeding birds.

Methods

Study site

Our study site was a concrete road bridge near Olpe, North Rhine-Westphalia, Germany (51°02′28″N 07°49′36″E; 325 m above sea level), which harboured a Swift colony comprising 42–48 breeding pairs (Wellbrock *et al.* 2017). The nest sites were located in hollow chambers beneath the carriageway. Birds entered and left the chambers through ventilation holes in the floor.

Geolocators

Our study was exclusively based on data from light-level geolocators. In total, we applied 20 geolocators to 16 Swifts at the colony at the end of the breeding season in 2012 and 2013 (ten geolocators applied per year with four individuals tagged in both years). We used the models MK 5540 (2012) and ML 6590 (2013) from Biotrack Ltd., Wareham, UK. The loggers were attached to the birds' back using a full-body harness made from polyester braided cord (British Trust for Ornithology, Thetford, UK; Wellbrock *et al.* 2017). Logger and harness altogether weighed on average 0.73 g (range: 0.66–0.80 g), representing 1.71% of the birds' weight (range: 1.51–1.93%). In 15 out of all 20 cases, the tagged birds returned to the colony in the year after tagging. The apparent survival of the tagged birds (75.0%) was slightly higher than in the control group of 52 birds which were captured and ringed but not tagged in 2012 and 2013 (67.3%). In eleven cases (ten birds), the returning tagged birds could be recaptured one or two years after tagging in order to detach the loggers and collect the data. In one case, the geolocator did not contain data from the breeding season and could therefore not be included in the present study. The data comprised 11 individual breeding seasons (hereafter termed bird-seasons) from 10 birds (one bird with two recorded bird-seasons; see online Appendix S1, Table S1 for details on sampled birds) from the years 2013–15 with a total of 686 individual sampling days (hereafter termed bird-days). Two of the ten birds were breeding partners (Appendix S1, Table S1).

The light values were supplied in arbitrary logger units ranging from 0 (no light) to 64 (full light). The time interval between successive light measurements of the geolocators was two minutes, which implies that there was a certain probability of missing nest visits shorter than two minutes. However, nest visits of Swifts are relatively long, even in the chick-rearing phase (mean durations of 7–23 minutes during chick-rearing; Arens 2011a, 2011b). Data on nest visit duration based on video material from our colony (Welzel 2011, Klenner 2014) suggested that during the nestling phase, only 8–16% of nest visits could stay undetected with our geolocator-based method due to a short duration of the stay at the nest site.

Interpretation of light data

Swifts are highly aerial: if not inside their nesting cavity, they spend daytime flying in the open airspace, foraging for aerial insects (Cramp 1985). Therefore, it is reasonable to interpret every bout of darkness recorded by a geolocator during daytime as a nest visit. The frequency distribution of daytime light values recorded by the geolocators was strongly bimodal, with 93.7% of values being either 0 (no light) or 64 (full light; Figure 1(a); online Appendix S2, Table S2). Arrivals at and departures from nests could easily be identified via abrupt changes in the light level (Figure 1(b); Appendix S2, Table S3). Gradual light changes during twilight (Figure 1(c)) were not classified as nest visits (see Appendix S2 for details on the data processing algorithms). The raw light-level data were transformed to nest visit data (times of arrivals at and departures from nest) using a self-written script in the program *R*, version 3.2.3 (R Core Team 2015), and the *R* package *chron*, version 2.3–51 (James & Hornik 2017).

Breeding phases

All tagged Swifts were adult breeding birds. Nests were visited every two days in order to record breeding progress. For every nest, the breeding season was divided into six phases: pre-breeding (before egg-laying), incubation, feeding 1–3 (feeding phase subdivided into 3 periods of 15 days each), and post-breeding (after fledging or nest failure). Medians of key dates of the bird-seasons considered in this study were 25 May for egg-laying ($n = 11$), 15 June for hatching ($n = 7$) and 25 July for fledging ($n = 6$).

Weather data

Daily means of ambient temperature and wind speed as well as daily sum of rainfall for each bird-day were provided by the weather station 'Olpe/Biggesee' owned by the City of Olpe situated about 1 km away from the study site (data retrieved from www.pannekloepper.de/wetterstation-olpe). For 18 bird-days, data on rainfall was not available. Medians of the three weather variables across all bird-days were 13.4°C for temperature (1st quartile [Q_1]: 11.0, 3rd quartile [Q_3]: 16.9), 5 km/h for wind speed (Q_1: 4, Q_3: 6) and 0.0 mm for rainfall (Q_1: 0.0, Q_3: 2.9).

Statistical analyses

Variation of nest visit frequency across the breeding season and in relation to weather conditions

In order to investigate the variation of nest visit frequency across the breeding season and in relation to weather conditions, we applied generalized linear

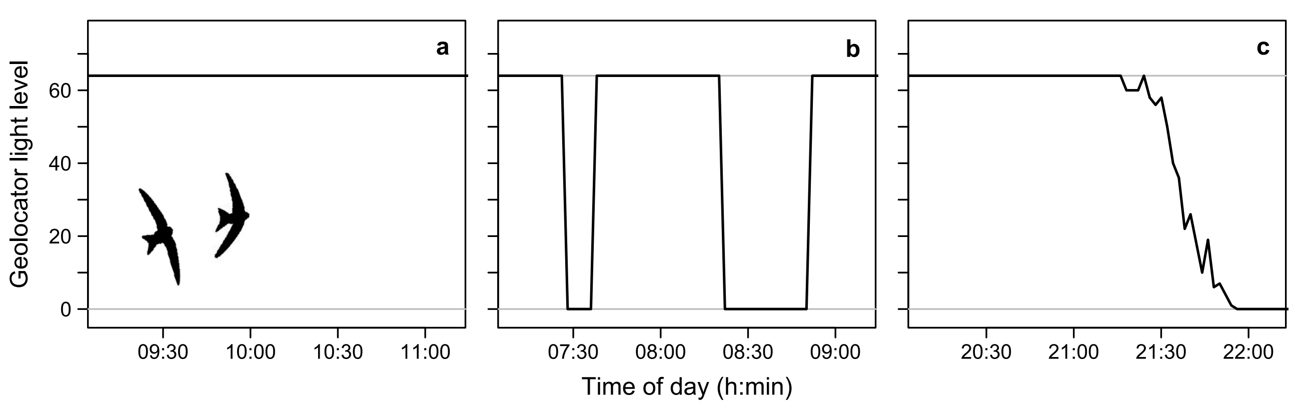

Figure 1. Examples of light-level sequences (arbitrary logger units) from geolocators fitted to Swifts, showing (a) continuous flight during daytime, (b) two nest visits (light value of zero), and (c) an evening when the bird was still on the outside during dusk. Grey horizontal lines: minimum and maximum light levels.

mixed models (GLMMs) with the number of daily nest visits as the dependent variable using a Poisson error distribution and the log link function. The day length in hours was used as an offset. As day of the year and average daily temperature were correlated ($r = 0.65$; $P < 0.001$; $n = 684$), we ran two separate models: one with only the day of the year as explanatory variable ('season model') and one with daily mean temperature, daily mean wind speed, daily sum of rainfall (z-transformed variables) and all three two-way interactions between these variables ('weather model'). In the 'season model', we included orthogonal polynomials up to the third degree because we expected a maximum of nest visit frequency in the first part of the feeding phase (Arens 2011a, 2011b). In both models, the bird-season identity was considered as a random effect (random intercept) to account for individual and year-wise variation (including number of chicks). In the 'weather model', the individual breeding phase was included as an additional random effect (random intercept). The models were fitted in *R* using the function *glmer* from the package *lme4*, version 1.1–14 (Bates *et al.* 2015). The model assumptions were assessed graphically and we checked whether overdispersion was present by using the function *dispersion_glmer* from the *R* package *blmeco*, version 1.1 (Korner-Nievergelt *et al.* 2015).

As recommended by Bolker *et al.* (2009), we used Bayesian methods to calculate 95% credible intervals (CrI) for the parameter estimates and model predictions following the methods described in Korner-Nievergelt *et al.* (2015). We applied the function *sim* from the R package *arm*, version 1.9–3 (Gelman & Su 2015) to obtain a sample of 2000 simulated values from the joint posterior distribution of the model parameters. The means of the simulated values of the model parameters were used as estimates, and the 2.5% and 97.5% quantiles as lower and upper limits of the 95% CrI. Non-informative prior distributions were used. A parameter was considered to be significantly different from zero if its 95% CrI did not include zero.

Diurnal variation of nest visit frequency

In order to investigate the variation of nest visit frequency during the course of the day, we calculated the average number of nest visits per hourly bin of daytime for each of the different breeding phases. Besides using the absolute local time of day (Central European Summer Time, CEST), we also applied the time relative to sunset and sunrise.

Encounter probability

To provide a basis for developing specific guidelines for efficient monitoring of potential Swift nest sites, we used the geolocator data to calculate the probability of encountering Swifts arriving at or leaving the nest when observing an effectively occupied nest site. A time window – representing a hypothetical observation bout at the nest site – with variable duration (0.5, 1.0, 1.5 and 2.0 h) was moved throughout the course of the day with an increment of one minute (again both applying absolute local time and time relative to sunrise and sunset). For every time window, we calculate the encounter probability from the geolocator data in two different ways: a) based on arrivals at the nest only (probability of occurrence of at least one arrival) and b) based on arrivals at and departures from nest (probability of occurrence of at least one arrival or departure). This was done by dividing the number of bird-days where (a) at least one visit or (b) at least one visit or departure was recorded by the geolocators within the considered time window by the total number of sampled bird-days (averaging over all individuals). We used these two different approaches because departures are more difficult to spot for an observer than arrivals, especially when several potential nest sites are monitored at the same time (see Discussion). On the one hand, we applied this procedure to those bird-days with conditions identified as leading to the highest number of daily nest visits ('best conditions' regarding date and weather), and on the other hand to all other bird-days.

These calculations provided probabilities referring to single individuals (P_{ind}). They were converted into probabilities for a hypothetical breeding pair (P_{BP}), i.e. the probability of observing at least one nest visit (or departure) by at least one of the breeding partners, by calculating the sum of the probability that both partners arrive at (or depart from) the nest during the given observation bout, the probability that partner 1 arrives (or departs) and partner 2 does not, and the probability that partner 2 arrives (or departs) and partner 1 does not, assuming equal arrival/departure probabilities for both breeding partners ($P_{ind\_1} = P_{ind\_2}$): $P_{BP} = P_{ind\_1} \times P_{ind\_2} + P_{ind\_1} \times (1 - P_{ind\_2}) + (1 - P_{ind\_1}) \times P_{ind\_2}$. We aimed for identifying circumstances providing an encounter probability of more than 90% for a breeding pair.

Results

In total, we identified 3862 nest visits based on the geolocator data, resulting in an overall mean of 5.63 visits per bird-day (median: 5, range: 0–20, Q_1: 3, Q_3: 8), i.e. 0.32 visits per hour of daylight (median: 0.29, range: 0.00–1.15, Q_1: 0.17, Q_3: 0.45). The average duration of identified nest visits was highest during the main incubation period (median of 56 minutes in 1st June decade) and declined afterwards (median of 4 minutes in 3rd July decade; online Appendix S3, Figure S1).

Variation of nest visit frequency across the breeding season and in relation to weather conditions

The number of daily nest visits increased from the pre-breeding phase to a maximum in the first 30 days of chick-rearing (phases 'feeding 1' & 'feeding 2'), declining again towards the time of fledging (Figure 2; Table 1). Accordingly, following the 'season model', the number of visits reached its minimum (0.24 visits per hour; 95% CrI: 0.20–0.28) on 10 May (CrI: 26 April–16 May) and its maximum (0.40 visits per hour; CrI: 0.34–0.46) on 3 July (CrI: 1 July–6 July; Figure 3(a); Table 1).

Ambient air temperature had a positive effect on the number of daily nest visits and the largest effect size amongst the considered weather variables (Figure 3(b); Table 1). Both rainfall and wind speed had a negative effect on the number of visits (Figure 3(e and f)). The effect of rainfall was more pronounced at low temperatures, while at high temperatures, the modelled mean number of visits was as high during moderate rainfall as in dry weather (Figure 3(c); significant interaction between temperature and rainfall; Table 1). Wind speed affected the number of visits mainly during warm weather, and high wind speeds buffered the positive effect of temperature (Figure 3(d); significant interaction between temperature and wind speed; Table 1).

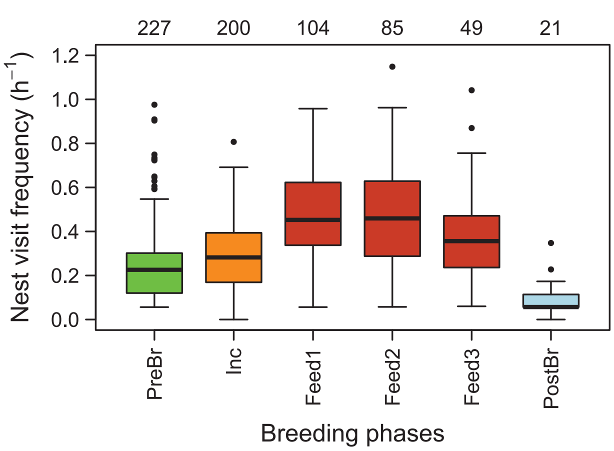

Figure 2. Nest visit frequency of individual Swifts (per bird-day) in different phases of the breeding season based on geolocator data. PreBr = pre-breeding, Inc = incubation, Feed = feeding (subdivided into three phases), PostBr = post-breeding. Thick horizontal lines: medians; boxes: 1st and 3rd quartiles; whiskers: lowest and highest data points within 1.5 times the inter-quartile range from the nearest quartile; points: outliers. Numbers above graph: sample sizes in terms of bird-days.

Based on these results, the best observation conditions for use in the subsequent analysis were defined as follows: days within 21 days around the modelled maximum of daily nest visits (23 June to 13 July) which were warmer, had less rain and less wind than the mean across all bird-days (temperature > 14.06°C, rainfall < 2.59 mm and wind speed < 5.13 km/h).

Diurnal variation of nest visit frequency

Regarding the variation of nest visit frequency during the course of the day, we detected the same general pattern in all breeding phases: an increase during the early morning, a plateau in the later morning and around noon, a low in the afternoon, and a distinct peak in the evening (Figure 4). In the feeding phase, the plateau of nest visit frequency was reached earlier in the morning than in the pre-breeding and incubation phase, both regarding the absolute time of day (Figure 4(a)) and the time relative to sunrise (Figure 4(b)). The afternoon low was most pronounced in the pre-breeding phase (Figure 4(a)). The evening peak (up to 1.07 visits per hour in the feeding phase) was found in the hour around sunset in the incubation and feeding phase, whereas – relative to sunset – it was earlier in the pre-breeding phase (Figure 4(b)).

Encounter probability

The calculated encounter probability based on arrivals at nest generally followed the same daily pattern as the nest

Table 1. Overview of parameter estimates with 95% credible intervals (CrI) of generalized linear mixed models of the number of daily nest visits of Swifts in relation to the day of the year and weather conditions based on geolocator data.

		Parameter estimate		
	Variable	2.5% quantile	Median	97.5% quantile
'Season model'	(Intercept)	−1.341	−1.181	−1.024
	DOY (linear)	2.757	3.781	4.733 *
	DOY (quadratic)	−2.948	−2.080	−1.226 *
	DOY (cubic)	−3.152	−2.250	−1.332 *
'Weather model'	(Intercept)	−1.719	−1.322	−0.928
	Temp	0.103	0.144	0.183 *
	Rain	−0.160	−0.118	−0.078 *
	Wind	−0.104	−0.071	−0.034 *
	Temp:Rain	0.002	0.044	0.088 *
	Temp:Wind	−0.086	−0.048	−0.011 *
	Rain:Wind	−0.045	0.000	0.043

DOY = day of the year, Temp = daily mean temperature, Rain = daily sum of rainfall, Wind = daily mean wind speed. *Significant variables (CrI not including zero).

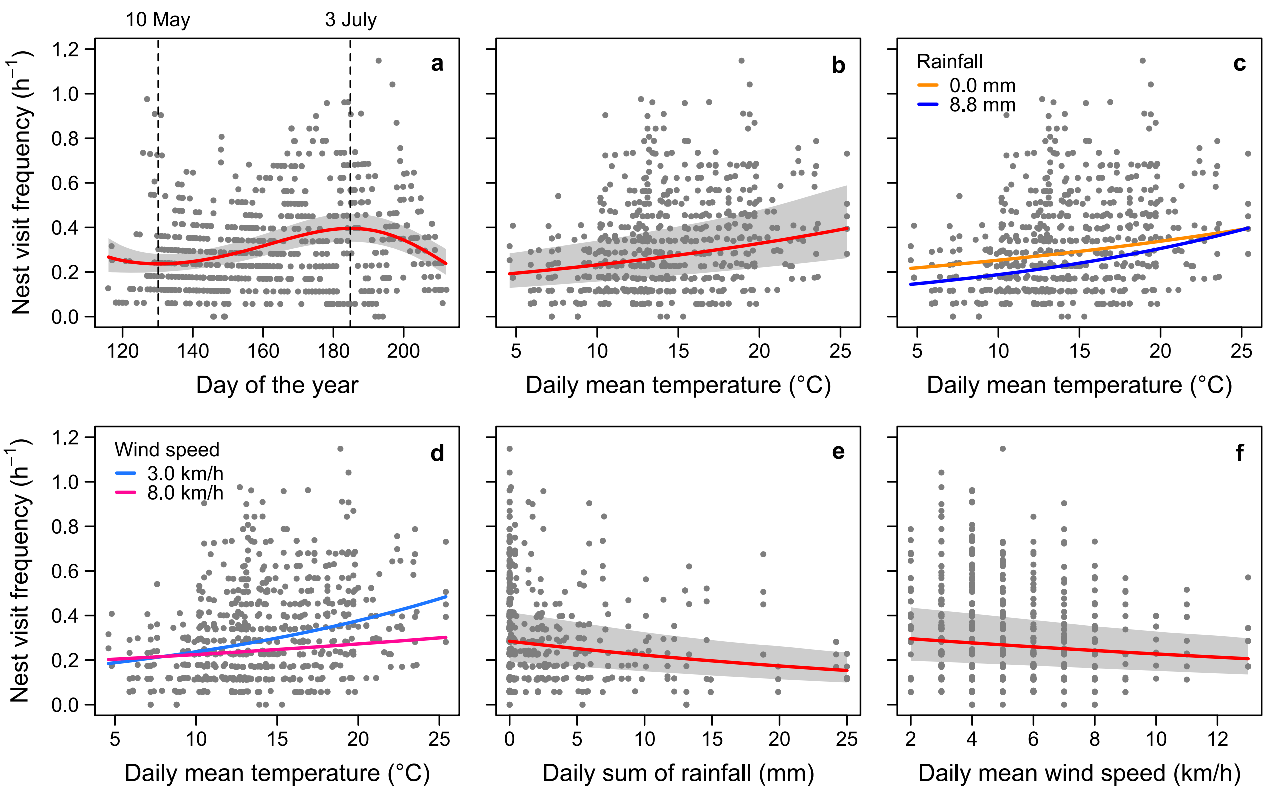

Figure 3. Relationship between the nest visit frequency of individual Swifts (per bird-day) and (a) day of the year, (b) temperature, (c) temperature under different rainfall conditions, (d) temperature under different wind conditions, (e) rainfall, and (f) wind speed, as resulting from GLMMs based on geolocator data. Grey polygons: 95% credible intervals. Sample sizes: 686 bird-days for (a) and 668 bird-days for (b–f). Selected values for rainfall and wind speed in (c) and (d) represent the respective 10th and 90th percentile across all bird-days.

visit frequency (Figure 5(a); online Appendix S4, Figure S3a). When also considering departures from nests, the encounter probability was further increased in the morning and afternoon (additional peak about three hours after sunrise; Figure 5(d), Figure S3d). However, in the evening, the encounter probability was as high when only considering arrivals as when both arrivals and departures were taken into account (Figure 5(a and c); Figure S3a and c). In the evening from about three hours before sunset onwards, the 90% threshold of encounter probability was exceeded in all cases, even with a time window of only 0.5 h when starting an

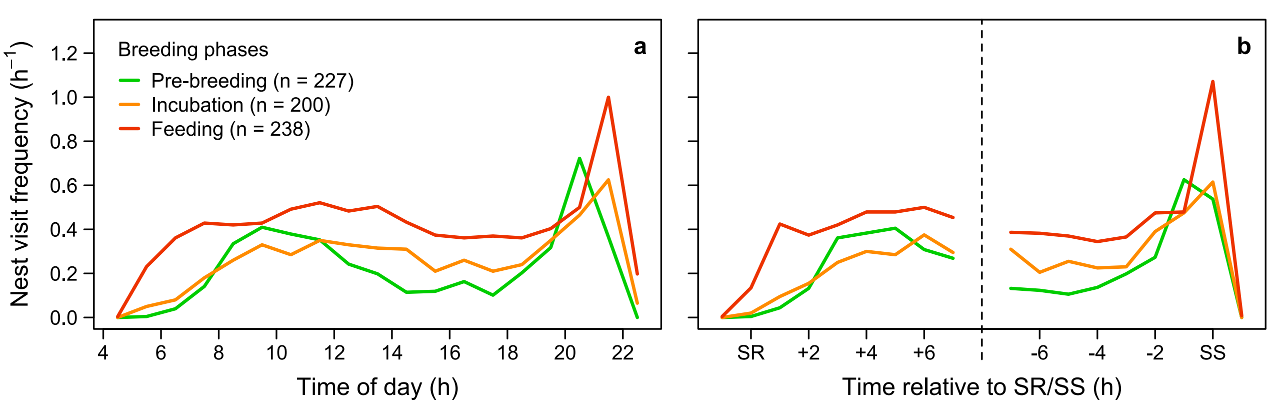

Figure 4. Nest visit frequency of individual Swifts over the course of the day in different phases of the breeding season based on geolocator data, with (a) referring to local time (CEST; 4 AM to 10 PM) and (b) to time relative to sunrise (SR) and sunset (SS), both applying hourly bins. Values are indicated at the centre of the time span which they represent. Note the discontinuous *x*-axis in (b). The post-breeding phase was not considered due to the small sample size. Sample sizes are given in terms of bird-days.

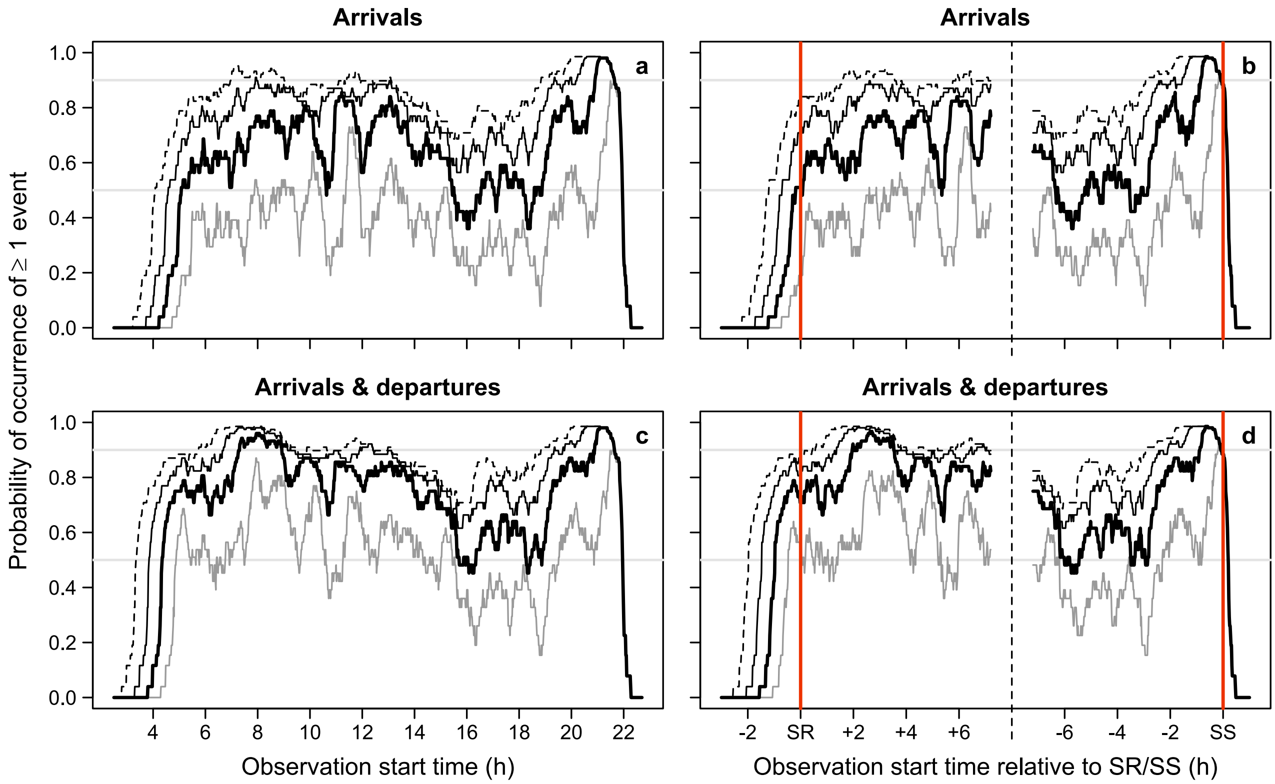

Figure 5. Encounter probability of Swifts at the nest site over the course of the day under best observation conditions (see below) based on geolocator data ($n = 50$ bird-days), applying hypothetical observation bouts of different lengths. The *y*-axis indicates the probability of occurrence of at least one event (only arrivals at nest or both arrivals and departures considered). The *x*-axis indicates the start time of observation bouts, either in local time (CEST; a, c) or in time relative to sunrise (SR) and sunset (SS; b, d). Note the discontinuous *x*-axis in (b) and (d). Bout length: 0.5 h (light grey curves), 1.0 h (thick black curves), 1.5 h (thin black curves), and 2.0 h (dashed curves). Light grey horizontal lines: encounter probability of 50% and 90%. Thick vertical lines in (b) and (d): sunrise and sunset. Best observation conditions: 23 June–13 July; daily mean temperature > 14.1°C; daily sum of rainfall < 2.6 mm; daily mean wind speed < 5.1 km/h.

observation bout shortly before sunset under best conditions (Figure 5(b and d)). Also in the morning and early afternoon, our geolocator data indicated suitable circumstances for nest site monitoring, e.g. when starting an observation bout of 1.0 h length between 2.0 and 3.5 h after sunrise under best conditions (considering arrivals and departures; Figure 5(b)).

Discussion

Using data from light-level geolocators, we showed that the nest visit frequency in Swifts varied across the breeding season and in relation to time of day and weather conditions. Based on these results, we determined time windows with a high probability of encountering nest visits, providing a sound basis for developing a monitoring protocol for reliable and time-efficient field observations at potential Swift nest sites. Most importantly, these data allowed us to specify how long observation bouts need to last to provide a sufficient encounter probability under different conditions and at different times of day. This information was not available in earlier recommendations for surveys of nest sites of Swifts (Andretzke *et al.* 2005, Ferguson-Lees *et al.* 2011, Rijksdienst voor Ondernemend Nederland 2014). In general, the nest visit frequency we found in Swifts was distinctively lower than in similar-sized species of other bird families (Fournier & Arlettaz 2001, Freitag *et al.* 2001, Rouaiguia *et al.* 2015, Michalczuk & Michalczuk 2016), implying that nest monitoring is more time-consuming in Swifts.

Method validation

In our study, the overall nest visit frequency in Swifts was similar compared to earlier investigations (Lack & Lack 1951, Lack & Owen 1955, Carere & Alleva 1998, Arens 2011a, 2011b), indicating the general reliability of our geolocator-based method. However, during chick-rearing, we detected about 1.5 visits per day less than studies relying on transponder-antenna systems (underestimation by 16%; Arens 2011a, 2011b; online Appendix S3, Figure S2). This might be due to nest visits being shorter during this period compared to earlier breeding phases (Appendix S3, Figure S1; Arens 2011a), which entails a higher probability of non-detection with the 2 minutes measurement interval of the geolocators. Video material from our colony (Welzel 2011, Klenner 2014) also suggested that during the nestling phase, 8–16% of nest visits could stay undetected with the geolocator-based method. The underestimation of nest visit frequency during chick-rearing implies that our recommendations for durations of field observation bouts during this period (see below) are conservative, i.e. precautionary.

It should be noted that we analysed the effect of weather on nest visit frequency only on a daily basis. As Swifts may compensate for bad weather during one part of the day by increased activity during other parts of the day, an analysis on a finer (e.g. hourly) scale would probably show the weather effects more clearly (increased effect sizes).

During the chick-rearing phase, another factor which might affect the nest visit frequency is the number of nestlings (Lack & Lack 1951, Carere & Alleva 1998). However, we have not considered this variable explicitly in our analysis (but implicitly by incorporating the individual breeding season as a random effect in the statistical models), because in practice, it cannot be taken into account by the observer of a potential Swift nest site.

Variation of nest visit frequency across the breeding season and in relation to weather conditions

The daily number of nest visits in Swifts was highest in the first 30 days of the nestling period, as found in earlier studies (Arens 2011a, 2011b). The following decrease of nest visit frequency (i.e. feeding frequency) goes along with Swift nestlings reaching the peak of their body mass in the fourth week after hatching, decreasing their weight by about 20% in the remaining two weeks before fledging (Lack & Lack 1951, Weitnauer 1980).

It is well-known that the availability of airborne insects depends on weather conditions (Freeman 1945, Grüebler *et al.* 2008, Cusimano *et al.* 2016). Therefore, feeding activity and breeding success of aerial insectivorous birds vary largely with weather (Lack & Lack 1951, Winkler *et al.* 2013, Lemke 2014, Arbeiter *et al.* 2016). In the present study, we could confirm a positive effect of air temperature and negative effects of rainfall and wind speed on the number of daily nest visits in Swifts. These may be explained by reduced availability of aerial insects under adverse weather conditions, which, in turn, leads to decreased flight activity in Swifts (birds remaining inside the nesting cavity for prolonged periods; Weitnauer 1947, Lack & Lack 1952). For Alpine Swifts *Tachymarptis melba*, Lemke (2014) also found effects of temperature and rainfall on the number of nest visits and a significant interaction between these variables. The latter suggests that even on rainy days aerial insect availability may be considerable, given that the air temperature is high. However, we stress that we actually cannot disentangle the effects of day of the year and temperature due to collinearity between these variables.

Diurnal variation of nest visit frequency

The nest visit frequency in Swifts followed a distinct pattern over the course of the day, with morning/noon plateau, afternoon low and a peak in the evening around sunset. Arens (2011a, 2011b) found a similar daily pattern. Lack & Owen (1955) reported a distinct peak of nest visit frequency between 11:00 and 12:00 followed by a sharp decrease during good weather, which contrasts with our finding of a constant level between 08:00 and 14:00 (Figure 5(c)).

The increase of nest visit frequency during the morning may probably be explained by increasing availability of aerial insects alongside rising air temperatures (Cucco & Malacarne 1996, Sahli 2016). Moreover, the first departures from nests after the night are delayed during bad weather in Swifts (own data, not shown; Weitnauer 1947, Keller 1977, Arens 2011a, 2011b), which contributes to a lower mean nest visit frequency in the morning.

The low of nest visit frequency in the afternoon was most pronounced during the pre-breeding phase. During this period, the afternoon low might possibly be explained by Swifts taking advantage of the high insect availability in the afternoon (Sahli 2016) for foraging and therefore restricting nest-related behaviours such as nest-building and mating to the morning. During chick-rearing, the (slight) drop in nest visit frequency in the afternoon could be due to nestlings being temporarily satiated by feedings during the morning and around noon, leaving the parents time for foraging for self-maintenance in the afternoon (Lack & Owen 1955).

The distinct peak in the evening in all breeding phases may to some degree be explained by the facts (a) that both breeding partners spend the night at the nest site in Swifts and (b) that the daily last arrivals at nest are tightly bound to the time of sunset, mostly taking place in the hour around sunset (own data, not shown; Arens 2011a, 2011b). Additionally, the start of activity in nocturnal insects presumably leads to good foraging conditions around sunset, even in bad weather (Kaiser 1992). Arens (2011a, 2011b), leaving the 'obligatory' last daily arrivals at nest unconsidered, found an evening peak only during the feeding phase. This suggests that during chick-rearing, the evening peak is due to both an increased feeding frequency as a result of good foraging conditions (possibly in combination with a high food demand of chicks before nightfall) and the last arrivals, whereas during other stages, it is solely caused by the last arrivals.

Recommendations for efficient nest site monitoring

Based on our analysis of nest visit frequency, we determined that the best conditions for observing potential nest sites of Swifts are present between end of June and mid-July on warm, dry and calm days. Under these circumstances, two relatively wide time frames (one in the morning and around noon, and another in the evening) are available which provide an encounter probability of more than 90% for a breeding pair with a single observation bout of 0.5–2.0 h (Figure 6). The best time of day for observing potential Swift nest sites is the period around sunset, providing a sufficient encounter probability with an observation bout of only 0.5 h under best conditions. When best conditions are absent, 1.5–2.0 h is necessary, and the possible time frames are smaller (Figure 6).

When many potential Swift nest sites situated close to each other are monitored at the same time by one observer, it is unlikely that birds leaving their nest site can be assigned to a particular nest site with certainty. Hence, in such situations, it is preferable only to rely on arrivals at the nest, which are easier to detect (first option 'no' in Figure 6).

It should also be noted that after sunset, it is advisable to perform observations at potential Swift nest sites only if the exact locations of the potential nest sites are known in advance (e.g. in the case of nest boxes). Otherwise, if entire building facades need to be kept in sight, the chance of overlooking nest visits may be considerable due to the bad light conditions.

Previous recommendations for the monitoring of potential Swift nest sites from the Netherlands were similar concerning the seasonal period and weather conditions, but imprecise concerning the required duration of observation bouts (Rijksdienst voor Ondernemend Nederland 2014). The same is true for

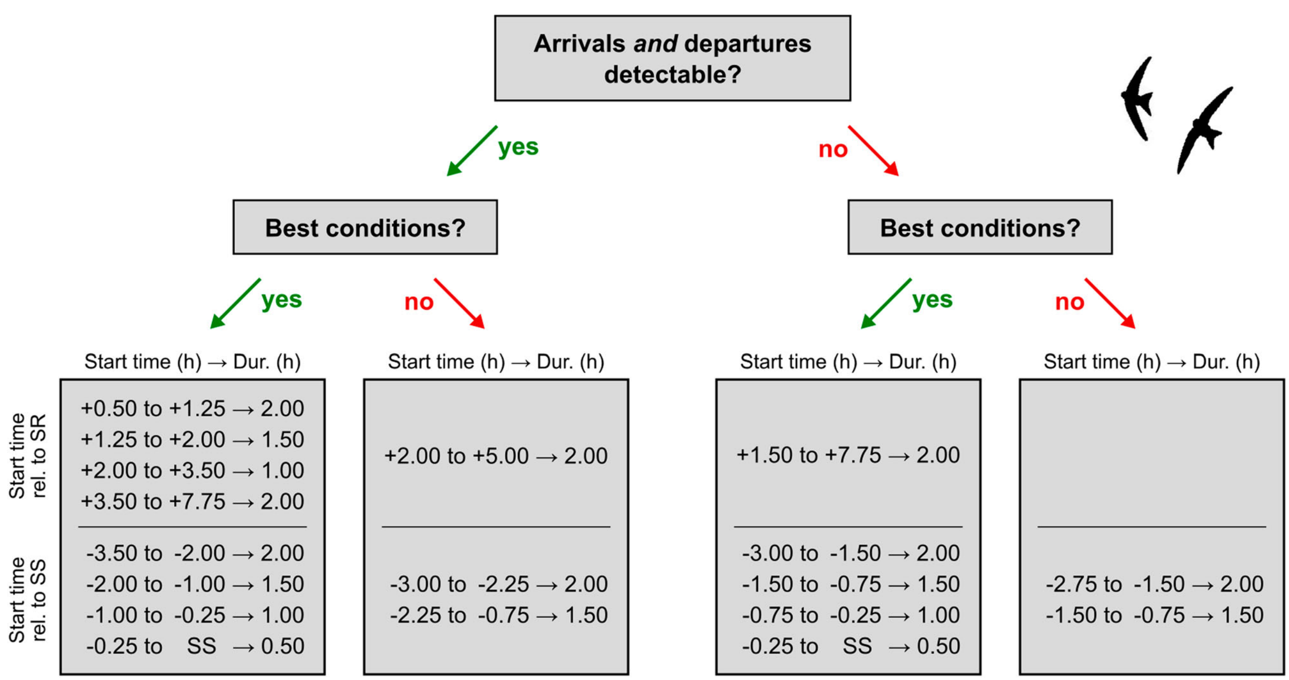

Figure 6. Scheme with recommended time windows for observing potential Swift nest sites providing an encounter probability greater than 90%. Start time ranges (left of the arrows) relative to sunrise (SR; morning/noon time windows) or sunset (SS; evening time windows) and the recommended duration of observation bouts in hours are indicated (right of the arrows). Thin horizontal lines inside boxes: limit between morning/noon and evening time windows. Best conditions: 23 June–13 July; daily mean temperature > 14.1°C; daily sum of rainfall < 2.6 mm; daily mean wind speed < 5.1 km/h.

survey methods in the UK (RSPB 2019). Another manual from Germany recommended observing potential nest sites during at least 30 minutes (Andretzke *et al.* 2005). Based on our geolocator data, we confirmed that 30 minutes is indeed the minimum duration of observation bouts. However, an observation bout of 30 minutes is only sufficient in very specific circumstances (around sunset in good weather between end of June and mid-July). In other circumstances, even two hours may not be sufficient to achieve an adequate encounter probability. Andretzke *et al.* (2005) suggested mid-May to the beginning of June as the monitoring period, which may be appropriate when Swift population sizes are to be estimated via counts of flying birds including breeders and non-breeders. However, we showed that this is not the most suitable period for locating nest sites based on arrivals and departures of breeding birds.

It is important to note that direct application of our recommendations is only possible within Central Europe: First, breeding phenology of Swifts varies according to climate, with earlier onset of egg-laying in warmer climate (Cramp 1985). This implies that the seasonal period for efficient nest monitoring of Swifts will start earlier in these regions. Second, latitudinal differences in light regime probably affect the diurnal variation of nest visit frequency. For example, at higher latitudes where twilight lasts longer, Swifts tend to roost later in relation to sunset (von Haartmann 1949). Third, when the daylight period lasts longer, the nest visit frequency might generally be lower, requiring longer observation bouts at potential nest sites. Therefore, regional nest attendance data is necessary to be able to give recommendations for observations at potential Swift nest sites in other regions.

Our recommended methodology is only based on breeding birds arriving at and/or departing from the nest site. However, it is clear that additional clues – such as faecal traces and birds looking out of the cavity's entrance hole or calling from inside the cavity – should also be taken into account in order to further increase the probability of detecting occupied nest sites.

It should be noted that observing Swifts entering or leaving a cavity does not necessarily imply the presence of an active nest inside the cavity, as prospecting non-breeders may also visit potential nest sites (often the sites where they will breed in the upcoming year; Genton 2010). However, the typical 'banging' behaviour of non-breeding Swifts normally only implies that the birds fly up to the entrance hole and shortly cling below it without entering the cavity (Lack & Lack 1952).

Conclusions

Geolocators are usually used to study bird migration. However, light data from geolocation may also be applied to investigate nest attendance in cavity-breeding birds, provided that the measurement interval of the geolocators is sufficiently small with respect to the duration of nest visits in the focal species. In this study, we showed that repurposing geolocator data in such a way can help to elucidate breeding behaviour and supply important information for bird conservation. Therefore, we want to encourage other researchers to make use of (already existing) geolocator data from other cavity breeders for similar analyses.

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