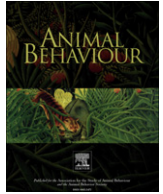


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Twilight ascents by common swifts, *Apus apus*, at dawn and dusk: acquisition of orientation cues?

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Common swifts are specialist flyers spending most of their life aloft, including night-time periods when this species roosts on the wing. Nocturnal roosting is preceded by a vertical ascent in twilight conditions towards altitudes of up to 2.5 km, behaviour previously explained as flight altitude selection for sleeping. We examined the nocturnal flight behaviour of swifts, as uniquely identified by a Doppler weather radar in central Netherlands using continuous measurements during two consecutive breeding seasons. Common swifts performed twilight ascents not only at dusk but also at dawn, which casts new light on the purpose of these ascents. Dusk and dawn ascents were mirror images of each other when time-referenced to the moment of sunset and sunrise, suggesting that the acquisition of twilight-specific light-based cues plays an important role in the progression of the ascents. Ascent height was well explained by the altitude of the 280 K isotherm, and was not significantly related to wind, cloud base height, humidity or the presence of nocturnal insects. We hypothesize that swifts profile the state of the atmospheric boundary layer during twilight ascents and/or attempt to maximize their perceptual range for visual access to distant horizontal landmarks, including surrounding weather. We compare twilight profiling by swifts with vertical twilight movements observed in other taxa, proposed to be related to orientation and navigation.

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Twilight (Rozenberg 1966) is an important cue in the daily cycle of most animals (Roenneberg & Foster 1997), marking the transition from diurnal to nocturnal behaviour. Shifting patterns in visibility, food availability and predation force many self-propelled animals to change their spatial niche around dusk and dawn, for example zooplankton (Hays 2003), insects (Åkesson et al. 2002; Narendra et al. 2010), fish (Helfman et al. 1982; Willis et al. 2009), birds (Alerstam 1990) and mammals (Kavanau & Peters 1976). For most birds, twilight typically coincides with transitions between activities associated with foraging, roosting or migration.

The common swift is a specialist flyer spending nearly its entire life on the wing (Lack 1956). In this respect, swifts are perfect model species for aeroecological research (Kunz et al. 2008). Foraging,

mating, even nocturnal roosting (Weitnauer 1952; Bruderer & Weitnauer 1972; Tarburton & Kaiser 2001) are performed in flight, possibly using unihemispheric sleep (Rattenborg 2006). The species only lands for short periods to breed (Lack & Lack 1951) and its extreme life of continuous flight poses strict constraints on morphology (Lentink et al. 2007; Henningsson et al. 2008), physiology (Koskimies 1948) and behaviour (Koskimies 1950; Lack 1956). Swifts have been shown to be remarkably adaptable in their movement patterns year-round. Being fully dependent on aerial fauna for foraging, proper assessment of weather conditions is crucial, and swifts may set out on extensive migrations for feeding when weather at the breeding site is unfavourable (Koskimies 1950; Lack 1956). As an aerial feeder and nonstop flyer, swifts are continuously confronted with movement decisions (more so than other species), especially during behavioural transition periods such as twilight.

Swifts often perform social flights in late evening in flocks called 'screaming parties' (Lack 1956; Henningsson et al. 2010). These

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flights continue until dusk, when the participating birds climb to high altitude (often in flocks, Lack 1956) and start roosting on the wing (Bruderer & Weitnauer 1972). In early summer these ascents are undertaken mostly by nonbreeding swifts, since breeding birds usually spend the night on the nest (Lack 1956; Tarburton & Kaiser 2001). There are indications that swift species other than *Apus apus* also indulge in similar dusk ascents (Tarburton & Kaiser 2001, and references therein).

Common swifts are highly capable of adaptive responses to wind, being so far the only species for which nocturnal wind drift compensation during migration has been demonstrated (Karlsson et al. 2010). An earlier study found that they did not select predicted optimal flight altitudes for roosting during dusk ascent (Bäckman & Alerstam 2001). It was reported that, contrary to predictions, common swifts did not select altitudes with slow or moderate winds that would minimize energy expenditure during the nocturnal flight. The apparent paradox of strong wind drift compensation during migration versus low wind selectivity during roosting illustrates that the dusk ascent of swifts is not well understood.

Buurma (2000) observed radar echoes of birds above large water bodies in the Netherlands ascending to high altitude not only at dusk but also at dawn. Several anecdotal field observations suggested swifts are the only likely source of these radar echoes. If swifts indeed climb to high altitude twice daily, the role of these ascents needs to be put into a new perspective.

Recently we developed a new automated method for bird detection using weather radar (Dokter et al. 2011) by which altitude profiles of aerial bird density can be determined. In this study we combined this method with additional wing beat detection to identify roosting swifts (Bruderer & Weitnauer 1972). Swifts leave characteristic signatures in weather radar data, which allowed us to compile a 2-year data set of swift flight altitudes in the breeding season. For this paper we analysed nocturnal flight altitudes of swifts in terms of timing and atmospheric conditions to shed new light on the purpose of their twilight ascents.

METHODS

Weather Radar Measurements

We used a C-band Doppler weather radar in conventional scanning mode to record swift flight altitudes in De Bilt, the Netherlands (52.11°N, 5.18°E). We also operated this radar in fixed-beam mode to record individual wing beat signatures for species identification, to our knowledge the first time an operational weather radar has been used for this purpose. Fixed-beam measurements and conventional measurements cannot be conducted simultaneously.

Bird Density Profiling

We used methods described by Dokter et al. (2011) to derive altitude profiles of bird density (ρ [birds/km²]) every 5 min during the breeding season of 2008 and 2009 (15 May–1 August). Altitude profiles were generated for birds and for clear-air echoes (including insects and aerial plankton). These echoes can be distinguished based on their different spatial velocity patterns, that is, in the bird-only profile, layers consisting of clear-air echoes with a radial velocity standard deviation $\sigma_r < 2$ m/s are discarded as nonbird echoes (see Dokter et al. 2011 for further details).

The volume reflectivity (η [cm²/km³]) measured by weather radar can be written as the product of bird density times a bird-specific radar cross section (RCS; Dokter et al. 2011). At low elevations the RCS for swifts is similar to that for passerines

(Schmaljohann et al. 2008). We therefore used the average RCS for passerines at C-band (i.e. $\sigma_{\text{swift}} = 11$ cm², see Dokter et al. 2011) to convert reflectivity to swift density.

The volume reflectivity caused by clear-air echoes unrelated to birds has been found to decay mostly exponentially with altitude (see e.g. Contreras & Frasier 2008). We assumed the altitude distribution of swifts during twilight ascents is well approximated by a normal distribution centred at altitude μ of width σ , which we considered a reasonable assumption given the observed reflectivity profiles during nights with limited insect scattering. We therefore decomposed each clear-air volume reflectivity profile into an exponentially decaying term and a normal term (Fig. 1), and took μ as the mean swift flight altitude. This procedure is more robust in separating swifts and insects when the swift layer descends into considerable insect scattering, as the radial velocity standard deviation criterion is not designed to deal with proportional mixtures of insect and bird scattering (Dokter et al. 2011).

Climb rates were determined in the period 10–25 min before and after reaching maximum altitude as the mean rate of change of altitude μ . Climb rates were thus calculated as mean rates over all individual birds present. To determine these rates the swift layer needs to remain distinguishable from insect scattering during the climb and descent phases, which can be problematic in the case of low ascents and/or strong insect scattering. Nights with limited insect scattering for determining climb rates were manually selected ($N = 46, 33, 52, 45$ for dusk ascent, dusk descent, dawn ascent and dawn descent, respectively).

Wing Beat Detection

We scheduled a dedicated measurement night on 29 June 2009 when we took fixed-beam measurements at four consecutive beam elevations (6°, 10°, 4.5° and 2°, respectively) to adjust the beam roughly to the mean altitude of the expected ascent pattern of swifts. We thus obtained time series $Z(r, t)$ of radar reflectivity as a function of range r and time t . We only retained echoes above a noise level of $Z/r^2 > 3 \times 10^{-28}$ m (which corresponds to –22 dBZ

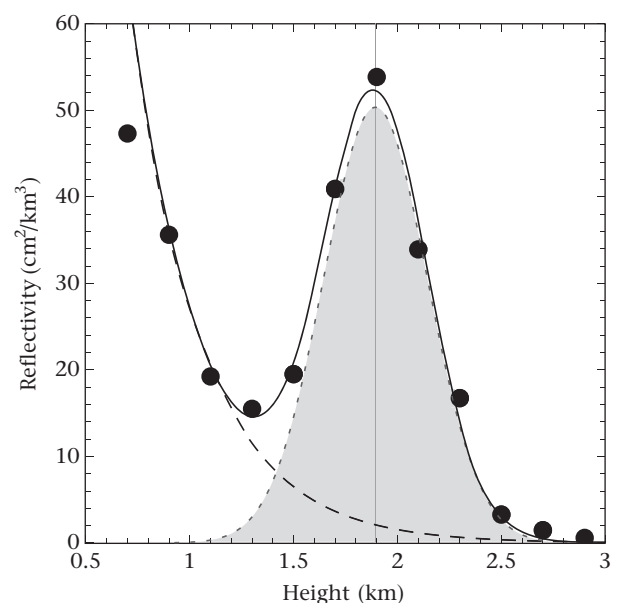


Figure 1. Volume reflectivity profile of 30 June 2009 2110 hours UTC (see Fig. 3) decomposed into an exponential term (dashed) and normal term (dotted). We defined the centre of the normal term μ as the swift layer height ($\mu = 1.8$ km in this example).

at 5 km range and -8 dBZ at 25 km range, sufficient to detect single birds over the entire surveyed volume). We retained echo signatures (Schmaljohann et al. 2008) of 10 s duration or longer, which were Fourier-transformed to obtain the wing beat frequency of each target.

Figure 2 shows an example of a detected signature together with its Fourier spectrum. This echo signature is highly characteristic for a swift, showing (1) a relatively low wing beat frequency around 8.3 Hz and (2) the alternation between gliding and flapping phases of varying length, which uniquely identifies the signature as a swift (Bruderer & Weitnauer 1972; Bäckman & Alerstam 2001). Targets were automatically identified as swifts when the Fourier spectrum showed a peak at 7.5 ± 1.5 Hz (and at 15 ± 3 Hz for the first Fourier overtone). The only other species groups having a wing beat frequency around 7.5 Hz are waders and waterfowl (Bruderer et al. 2010), which are highly unlikely to be present on mid-summer nights around the weather radar at these altitudes. Peaks in the Fourier spectrum were selected at frequency ranges at which the Fourier amplitude exceeded a baseline threshold, defined as the 5 Hz running average of the Fourier amplitude plus twice the full spectrum's amplitude standard deviation (see the dotted line in Fig. 2b). We only considered echo signatures in the altitude band 0.8–4.0 km to discard ground clutter signals at low altitudes.

Meteorological Data

We derived altitude profiles, to a height of 4 km, of wind speed (W [m/s]), temperature (T [K]), atmospheric pressure (P [mb]) and relative humidity (RH [%]) using data from the gridded HIRLAM atmospheric model (Undén et al. 2002). These data had a temporal resolution of 1 h, and were discretized vertically at fixed pressure levels separated by not more than 20 mb. We used data from the grid point nearest the centre of the De Bilt radar (33 km east at 5.64°E , 52.02°N). Relative humidity was converted to absolute humidity (AH [g/m^3]) using the curve for saturated water vapour as a function of pressure and temperature by Buck (1981).

Cloud cover was measured by a Vaisala CT75K LIDAR ceilometer at the Cabauw Experimental Site for Atmospheric Research (CESAR, data available through the CESAR Consortium, <http://www.cesar-database.nl>) located at 51.97°N , 4.926°E , 25 km to the southwest of the centre of the De Bilt radar. Cloud base height (CBH [m]) was calculated every 30 s with 15 m vertical resolution. We defined nightly cloud persistence (C_p) as the cumulative fraction of cloud base observations from 1 h before sunset to 2 h after sunset.

RESULTS

Identification of Swifts in Weather Radar Data

Within the breeding season of common swifts (mid-May–late July, Lack 1956), weather radar data revealed distinct ascent patterns of birds during twilight (Fig. 3). We hypothesized that these ascent patterns are caused by roosting swifts, since migration is limited in summer and swifts are thus the only species likely to be aloft for roosting flights. To prove unambiguously that the observed ascent patterns were exclusively due to swifts, we recorded wing beat signatures of individual echoes and identified characteristic swift signatures as in Fig. 2.

Figure 3a shows the cruising altitudes of swifts identified in fixed-beam mode as green scatter points, overlaid on a reflectivity profile recorded in conventional operational scanning mode one night later. These two consecutive nights showed similar meteorological conditions and equal maximum ascent heights, as was verified by a conventional scan on the first night at 2110 hours UTC (the moment at which the ascent reached maximum height). The cloud of points clearly followed the reflectivity profile, demonstrating that the reflectivity profile contained swift echo signatures.

Of all detected echo signatures within the altitude band of 0.8–4.0 km, 46% were identified as swifts. Echoes by flocks of swifts show no clear wing beat frequency and cannot be identified by our method. Therefore flocks will make up at least part of the remaining 54% of nonswift echoes; however, this category also contains nonbird echoes, especially at the lower altitudes (see also Appendix Fig. A1). Nonbird echoes, presumably insects, made up the reflectivity profile that developed shortly after the dusk ascent of swifts at low altitude. Between 2055 and 2110 UTC the insect and swift patterns were still well separated and nonswift echoes were detected at a distinctly lower median altitude than swift echoes (1.2 ± 0.2 versus 1.9 ± 0.3 ; Mann–Whitney U test: $U = 3252$, $N_1 = 50$, $N_2 = 71$, $P < 0.001$; note that altitudes < 0.8 km were discarded in this analysis).

Figure 3b shows the bird-only reflectivity profile for 30 June 2009. We conclude that the ascending band of reflectivity was composed of swift echo signatures and we assigned equivalent ascent patterns on other nights also to roosting swifts.

Similarities Between Dusk and Dawn

In Fig. 4a a reflectivity altitude profile is shown for a full night within the swift breeding season. In addition to a dusk ascent

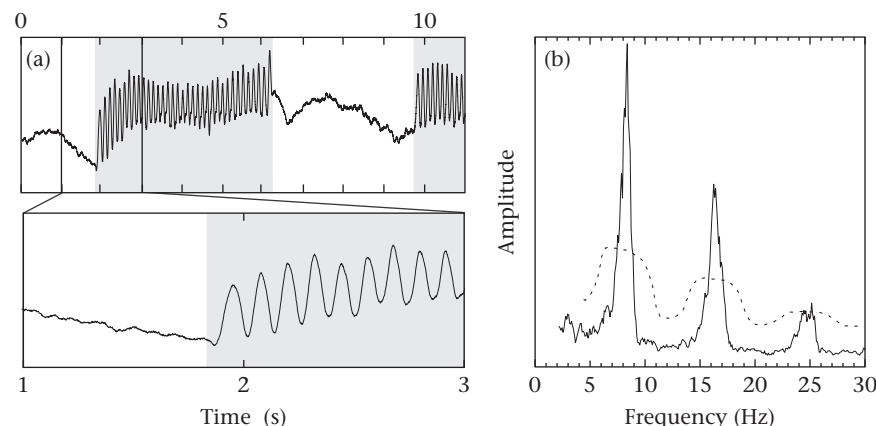


Figure 2. (a) Radar signature of a swift showing flapping and gliding phases, as recorded with Doppler weather radar operated in fixed-beam mode detected on 29 June 2009 2128 hours UTC at 21.6 km distance and 2.3 km height. Flapping phases are shaded in grey; gliding phases are unshaded. (b) Fourier spectrum of the same radar signature, showing a peak at a wing beat frequency characteristic for swifts (8.3 Hz in this example, and overtones at integer multiples). The detection threshold for Fourier peaks is drawn as a dotted line.

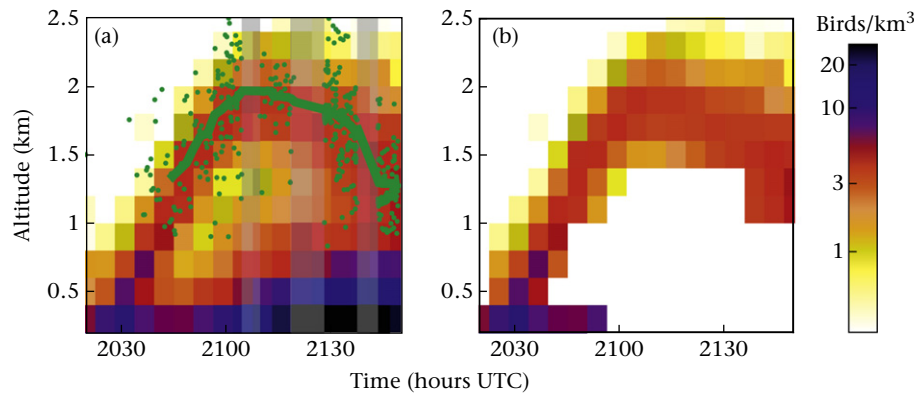


Figure 3. (a) Identified echo signatures of swifts (green dots, $N = 378$) as a function of time and altitude recorded in fixed-beam mode on 29 June 2009, overlaid on the reflectivity profile of clear-air echoes for 30 June 2009 (a night with very similar meteorological conditions and equal maximum ascent height). During grey-shaded periods fixed-beam measurements were temporarily interrupted to adjust the beam elevation. The solid green line gives the 10 min running average height of the swift signatures. (b) The bird-only reflectivity profile (Dokter et al. 2011) for 30 June 2009. Based on the fixed-beam measurements, we assigned this ascent pattern exclusively to swifts.

a second ascent pattern was visible around dawn. Swifts apparently made not only an evening/dusk ascent, but also a dawn ascent, unambiguously confirming the observations by Buurma (2000). Both ascents were timed with respect to sunset and sunrise as each other's approximate mirror images, reaching a maximum altitude during nautical twilight (solar elevation -6° to -12°). The similarity between the ascents is especially evident when the dawn ascent is displayed on a time-inverted axis and compared to the dusk ascent (Fig. 4b, c). The mirror symmetry is also evident from the comparable mean climb rates during the various ascent and descent phases, which equalled 0.8 ± 0.2 m/s ($N = 46$) for dusk ascent, -0.3 ± 0.1 m/s ($N = 33$) for dusk descent, 0.3 ± 0.2 m/s ($N = 52$) for dawn ascent and -0.6 ± 0.2 m/s ($N = 45$) for dawn descent.

Figure 5 shows at which solar elevation swifts reached their maximum ascent height. Only cases with limited or no cloud cover are shown ($C_p < 0.2$) to limit effects by clouds on the ascents and light condition. Maximum altitudes were reached at solar elevations between -5° to -9° at 40–70 min after sunrise and before sunset, depending on the altitude of the ascent. For nights with high ascents, the maximum altitude was reached later than on

nights with low ascents (ANOVA: $F_{2,50} = 38.9$, $P < 0.001$), as birds continued to climb for longer. Swifts also reached their maximum ascent height at dawn somewhat earlier on nights with high ascents than on nights with low ascents (ANOVA: $F_{2,31} = 8.0$, $P < 0.01$), in correspondence with the observed mirror symmetry between the ascents.

Effects of Atmospheric Condition on Ascent Height

The height of the twilight ascents varied considerably from day to day (Fig. 6a). Qualitative inspection of the general atmospheric conditions revealed that the highest ascents coincided with relatively warm nights and fair weather, in agreement with earlier studies reporting higher flight altitudes during roosting on warmer nights (Weitnauer 1960; Bäckman & Alerstam 2001). We tested which atmospheric variables correlated significantly with the maximum dusk ascent height h_{\max} by regressing a generalized linear model (GLM). As explanatory variables we tested relative humidity RH, absolute humidity AH, temperature T , wind speed W , all at altitude h_{\max} , as well as mean cloud base height CBH. Only temperature emerged as a significant explanatory variable,

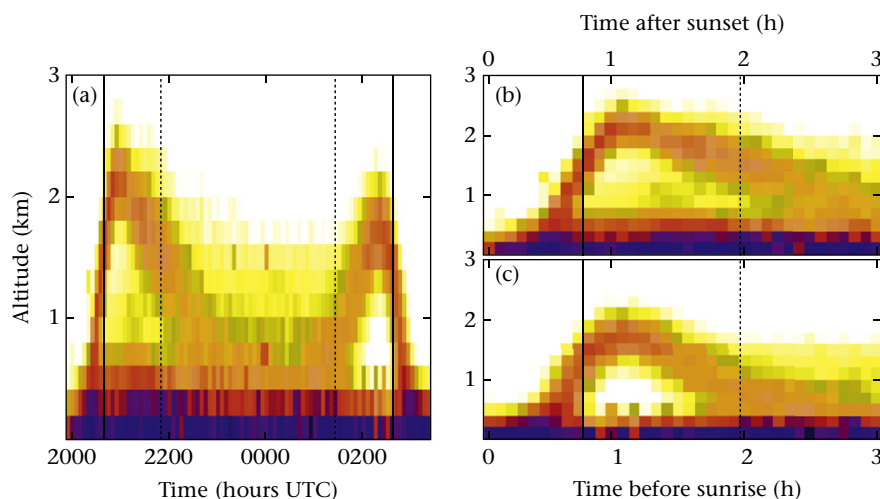


Figure 4. (a) Reflectivity altitude profile for the night of 1–2 June 2009, showing twilight ascents of swifts. In addition to the dusk ascent, swifts also participated in a dawn ascent. Both ascents were timed with respect to sunset and sunrise as each other's mirror images. (b) Dusk ascent, (c) time-inverted dawn ascent. The displayed time series started at sunset and ended at sunrise; solid vertical black grid lines indicate the transition between civil twilight and nautical twilight; dotted vertical lines indicate the transition between night and nautical twilight. Colour scale as in Fig. 3.

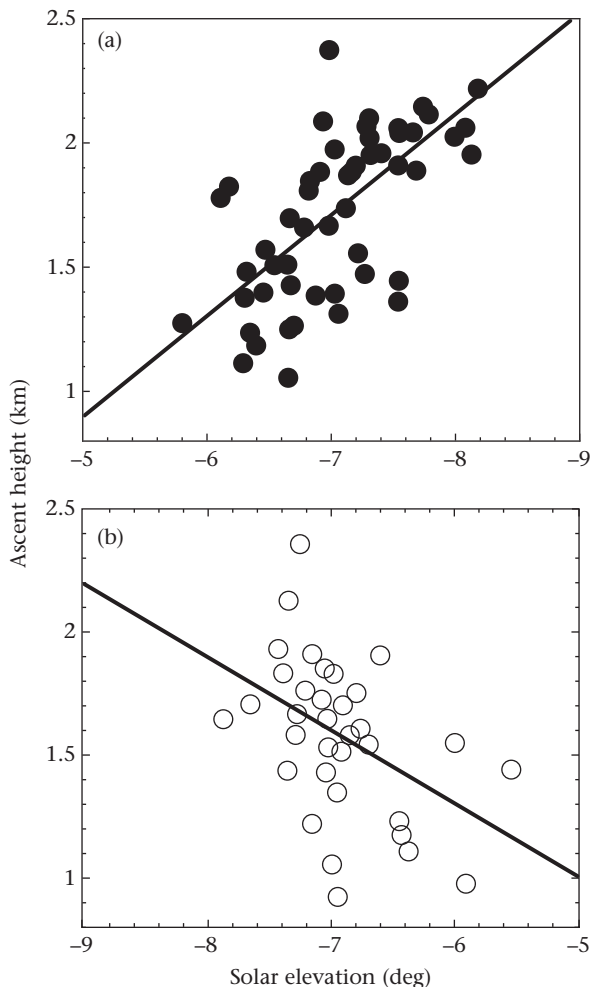


Figure 5. Altitude and solar elevation when swifts reached the maximum altitude during (a) dusk ascent and (b) dawn ascent in conditions with limited cloud cover ($C_p < 0.2$). Solid lines show linear least-square regressions.

showing a highly significant positive correlation with the maximum ascent height (Pearson $r = 0.47$, Student's $t_{92} = 5.1$, $P < 0.001$). Stepwise inclusion of other factors did not lead to a significant improvement of the model on a 1% significance level.

We tested the height of several isotherms (270–290 K) as explanatory variables for dusk ascent height (H_i [km], with i the corresponding isotherm in K). Models using the altitude of one of

the isotherms within the range 279–281 K as an explanatory variable had an equivalent likelihood (based on the criterion $\Delta AIC < 2$, see Burnham & Anderson 2002). Deviance explained for the best model (maximum ascent height $h_{\max} \sim 280$ K isotherm altitude) is 70%, showing a high correlation between ascent height and the 280 K isotherm height (Pearson $r = 0.84$, Student's $t_{92} = 14.6$, $P < 0.001$; Fig. 6b). Equivalent results were obtained for the dawn ascent, with an explained deviance of 63% for the best model ($h_{\max} \sim 282$ K isotherm altitude).

The maximum ascent height was very similar at dusk and dawn, although slightly lower at dawn (Student's t test: $t_{79} = 10.0$, $P < 0.001$) by on average 0.2 km. This difference was not explained by changes in atmospheric temperature (e.g. caused by nightly cooling), since overnight the 280 K isotherm shifted downwards only by a small amount (on average 0.06 km), which was not significant on a 1% level (Student's t test: $t_{79} = 2.38$, $P = 0.02$).

From late spring onwards, clear-air echoes related to insects become more prominent, which can be used to study the relative flight altitudes of swifts and their aerial prey. An example of a day with considerable radar scattering by insects is shown in Fig. 7. Clear-air reflectivity by insects shows a strong diurnal signal, with minima around sunrise and sunset and maxima at mid-night and mid-afternoon (Martin 2007; Contreras & Frasier 2008). Daytime reflectivity is fully dominated by insects and we cannot derive any bird flight altitudes at this time. On all nights we found that during the ascent phases swifts were flying above the insect scattering. In terms of timing, the dusk ascent of swifts was observed to start before the appearance of nocturnal insect echoes, and during the dawn ascent of swifts the band of insect scattering was already decreasing in altitude.

Discussion

Our observation that common swifts undertake twilight ascents not only at dusk but also at dawn casts new light on the purpose of these ascents. A twice nightly ascent pattern is inconsistent with the common implicit assumption that ascents occur as the onset or preparation of the birds' sleeping phase (Lack 1956; Bäckman & Alerstam 2001). In this context, the earlier observation that swifts are not selective for wind during roosting (Bäckman & Alerstam 2001) is in agreement with the idea that the ascents are unrelated to the sleeping phase itself, and that considerations other than minimizing overnight energy expenditure underlie the climb to high altitude.

Although from our data we cannot fully exclude nocturnal foraging by swifts around midnight (when swifts can reach altitudes below 600 m above ground level where insect scattering is

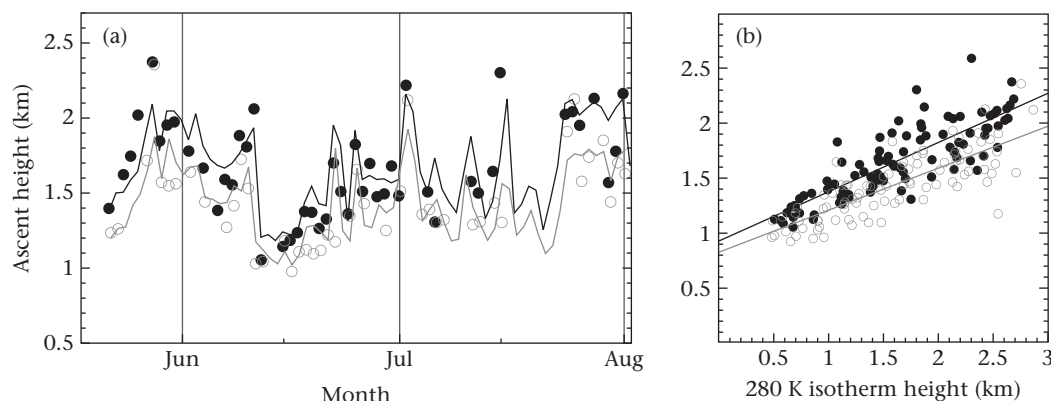


Figure 6. (a) Observed ascent height h_{\max} during dusk (closed circles) and dawn (open circles) for 2008. Linear model predictions of ascent height are drawn as solid lines (dusk: black, dawn: grey). (b) h_{\max} versus 280 K isotherm height (H_{280}) for 2008 and 2009. Solid lines indicate linear least-square regressions for the dawn and dusk ascent.

frequent), twilight ascents seem also functionally unrelated to foraging. This is illustrated most clearly at dawn, when swifts ascended while insects were observed to lower their flight altitude (see Fig. 7). This observation makes it unlikely that swifts were ascending to high altitude for aerial feeding.

Instead, the mirror symmetry of the dusk and dawn ascents with respect to sunset and sunrise strongly suggests that the ascents proceed in response to shifting ambient light levels. Observed climb rates were too low to assume that birds maintain a certain light regime by tracking the sun (and were also much lower than climb rates achieved by swifts operating near their maximum, 3–10 m/s, [Henningsson et al. 2010](#)). None the less, the ascents are likely to be functionally related to the twilight period, in particular nautical twilight, when our swifts reached their maximum ascent height.

Oriental mechanisms have been identified that rely on environmental cues only present during twilight. The magnetic compass of birds is calibrated by twilight cues ([Cochran et al. 2004](#)), in particular celestial polarization patterns ([Muheim et al. 2006](#)). These patterns show a maximum degree of polarization from sunset until the end of the nautical twilight period ([Rozenberg 1966](#); [Horváth & Varjú 2003](#); [Cronin et al. 2006](#)). Twilight is also the only period allowing simultaneous detection of landscape features, polarization patterns, stars and magnetic cues, making it a key period for combining information from different navigational systems ([Able & Able 1993, 1990](#); [Åkesson et al. 1996](#)).

We may thus hypothesize that the twilight ascents of swifts are also part of an orientational or navigational process, but one that benefits from high flight altitudes. Accordingly, we may formulate a new hypothesis on the purpose of swift twilight ascents: swifts use twilight ascents to assess their environment in terms of landscape and weather and accurately time these ascents at twilight when orientation cues are maximally available. The ascent flights may thus serve two simultaneous functions, namely assessment of the environment (in terms of landscape and/or atmospheric conditions) and perception of orientational or navigational cues.

What the environmental assessment entails and how it benefits from high flight altitudes may require different answers, depending on whether swifts ascend until meteorological conditions at high altitude become unfavourable (that is swifts behave as altitude maximizers), or alternatively ascend up to a specific or sufficiently high altitude that is required for a specific task (that is swifts behave as altitude profilers).

(1) Swifts as altitude profilers: assessing the atmosphere. The rapid ascent at dusk and the rapid descent at dawn could provide swifts with a direct vertical profile of one or more atmospheric variables, such as wind speed, direction and temperature. Birds may need to ascend to higher altitudes on warm nights if they want to probe the entire convective boundary layer (CBL). The extent of the CBL strongly correlates with daytime surface temperature ([Holton 2004](#)), the top being defined as the region in which the flow becomes geostrophic and is no longer directly influenced by the surface. Here, wind is determined by the relative positioning of surrounding synoptic pressure centres only ([Holton 2004](#)). High-altitude wind and temperature may therefore be more informative for assessing the position and course of surrounding synoptic centres, which determine the current and future weather conditions that so strongly influence the foraging success of swifts.

(2) Swifts as altitude maximizers: perceptual range maximization. The positive correlation between ascent height and atmospheric temperature may alternatively point to a strategy in which birds maximize their ascent height up to a physiological tolerance that correlates with temperature. By ascending from 0.1 to 2 km altitude, swifts increase their visual horizon from 35 to 160 km. The importance of perceptual range for movement decisions has been

recognized in landscape ecology as determining the connectivity of animals to remote patches ([Lima & Zollner 1996](#); [Olden et al. 2004](#)). At higher flight altitudes more distant landmarks become available to flying birds, including visual information on their dynamic landscape of surrounding weather. Distant clouds associated with fronts are easily recognizable as dark objects along the horizon ([Cronin et al. 2006](#)).

Future studies may be able to differentiate between altitude profiling and altitude maximizing, for example by studying the effect of the visibility of the horizontal landmark scene on the ascents. If factors that change visibility (e.g. low-level clouds or fog) do not affect ascent height, while local properties of the boundary layer do, then atmospheric profiling should be favoured over perceptual range maximization as the most likely mechanism underlying the ascents.

An important question deriving from our hypothesis is: what is the benefit of combining environmental assessment with the acquisition of orientational twilight cues? Information acquired through the ascents, such as the horizontal landmark scene, distant dynamic weather or the local state of the atmospheric boundary layer, might be referenced to the dynamic celestial polarization pattern, which has been shown to be an important calibration reference ([Muheim et al. 2006](#)). Under overcast and foggy conditions the highest degree of polarization is available near the horizon ([Hegedüs et al. 2007a, b](#)), suggesting under these circumstances a clear visibility of the horizon at high altitude would be beneficial for detection of the polarization pattern. Reference to a geographical compass system may be essential to interpret and make use of the information acquired during the ascents. For example, in the context of navigation challenges, environmental assessment may be combined with compass information to arrive at an optimal movement decision (e.g. to navigate towards favourable weather conditions for foraging). Also, in the absence of immediate navigation challenges, referencing to a compass system may be essential for consistent interpretation of the information acquired during twilight.

The caveat should be made that in this study flight behaviour of migratory and resident breeding birds could not be distinguished. Highest numbers of swifts are observed at nearby migration count sites in July (see <http://www.trektellen.nl>); therefore most migration and postbreeding dispersion coincided with the end of the local breeding season. After a few days in August, dusk and dawn ascents were no longer observed, but by then swifts had probably left the study area. Therefore the status of the twilight ascents during migration, when birds rely heavily on accurate navigation, remains unclear, and one should be cautious about generalizing observations of this study to outside the breeding period.

Comparable ascent behaviour has been described for various other species. A remarkable behaviour of migratory passerines is their so-called dawn ascent ([Myres 1964](#); [Richardson 1978](#); [Bourne 1980](#); [Diehl et al. 2003](#)), in which birds flying over open water climb rapidly to 1–2 km altitude at twilight, presumably to enlarge their perceptual range while reorienting with respect to celestial cues and visual landmarks. Passerines ([Åkesson et al. 1996](#)) may start migratory flight with an ascent during late dusk and both migratory ([Schmaljohann et al. 2011](#)) and premigratory ([Mukhin et al. 2005](#)) passerines were shown to undertake exploratory ascents within their home range at night and during twilight. These exploratory flights were suggested to be used to sense the atmospheric condition and relate landscape features to celestial and magnetic cues, in preparation for migration or while making a take-off decision.

For one animal in an entirely different taxonomic class, behaviour has been described that bears striking similarities with the twilight ascents of the common swift described here. The migratory southern bluefin tuna, *Thunnus maccoyii*, performs spike dives of up to 600 m in depth during twilight ([Willis et al. 2009](#)), which show

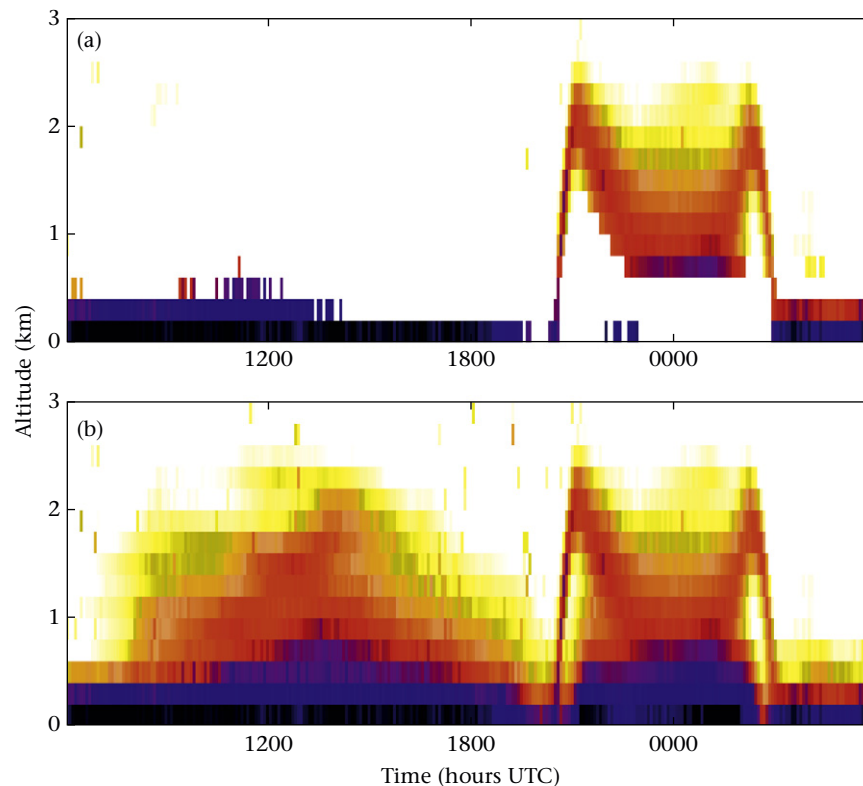


Figure 7. (a) Bird-only and (b) clear-air reflectivity altitude profiles for 25/26 June 2009. The clear-air profile includes echoes unrelated to birds, mainly arthropods such as insects.

an equivalent temporal mirror symmetry between the dawn and dusk dives as observed here for the twilight ascents of swifts. A similar idea was put forward that this behaviour is part of an orientation or navigation mechanism, in which twilight cues acquired at the surface are combined with information available only at certain depths, such as obtaining a referenced vertical profile of the oceanic currents.

If we assume that a common functionality underlies the twilight behaviour in both species, then an orientation/navigation process combined with simultaneous assessment of the medium of movement (air versus water) is consistent with both observations. The alternative hypotheses, that is, perceptual range maximization in the case of swifts and magnetic field estimation (free from disturbing currents at the sea surface, Willis et al. 2009) in the case of tuna, should then be discarded. In any case, the vertical movement patterns at twilight remain poorly understood for both species. Further quantification of the daily variations in visibility of the horizontal landmark scene, celestial cues and atmospheric conditions will be essential to link environmental factors to individual ascent behaviour and establish whether and how the carefully timed ascent flights of swifts are associated with navigation and orientation challenges.

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APPENDIX

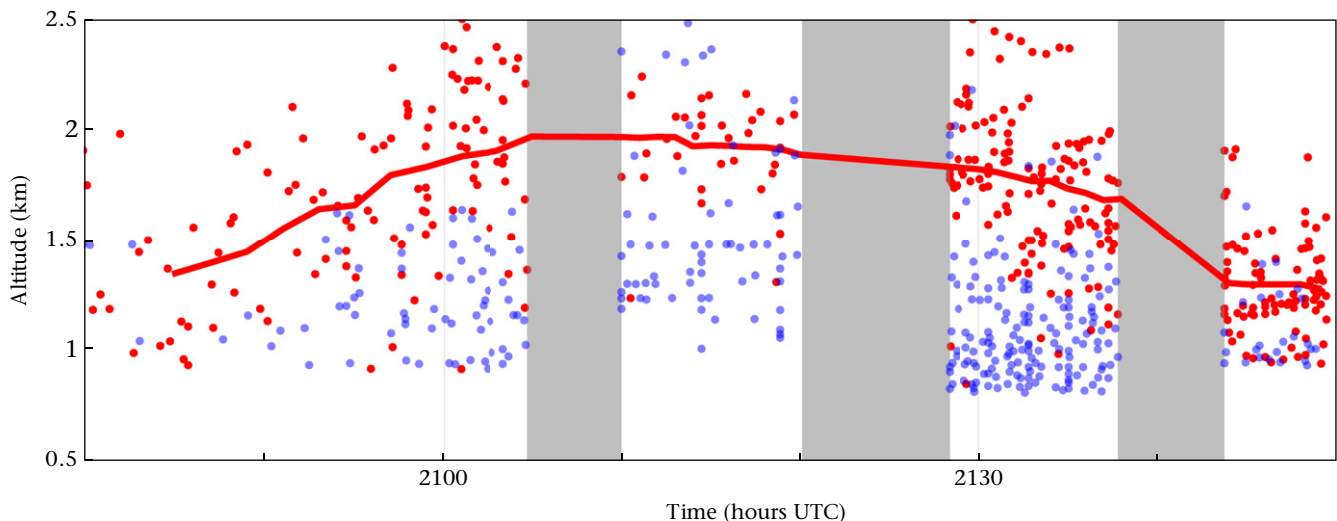


Figure A1. Identified echo signatures of swifts (red dots, $N = 378$) and echo signatures of nonswifts (blue dots, $N = 335$) as a function of time and altitude recorded in fixed-beam mode on 29 June 2009. During grey-shaded periods, fixed-beam measurements were temporarily interrupted to adjust the beam elevation. The red solid line gives the 10 min running average height of the swift signatures. The nonswift echo signatures also include signatures of swift flocks, which cannot be automatically identified because flock signatures do not reveal distinct wing beat patterns. Swift echoes are found on average above the nonswift echoes, which shows that swifts were ascending above the flight altitudes used by insects.