



## 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,

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 ( $\rho$  [birds/km<sup>2</sup>]) 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 ( $\eta$  [cm<sup>2</sup>/km<sup>3</sup>]) 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

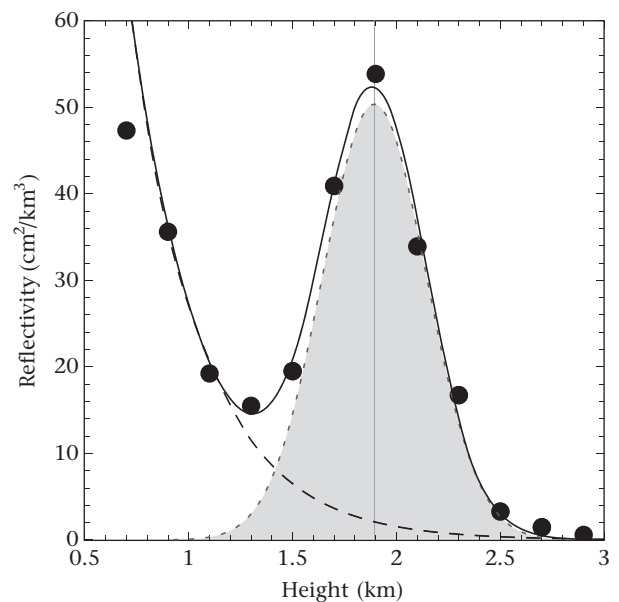
(Schmaljohann et al. 2008). We therefore used the average RCS for passerines at C-band (i.e.  $\sigma_{\text{swift}} = 11$  cm<sup>2</sup>, see Dokter et al. 2011) to convert reflectivity to swift density.

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  $\mu$  of width  $\sigma$ , 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  $\mu$  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  $\mu$ . 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  $\mu$  as the swift layer height ( $\mu = 1.8$  km in this example).

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