

Short communication

Flocking behaviour in the twilight ascents of Common Swifts *Apus apus*

CECILIA NILSSON^{1,2*}  JOHAN BÄCKMAN² & ADRIAAN M. DOKTER^{1,3}

¹Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Rd, 14850 Ithaca, NY, USA

²Department of Biology, Lund University, Sölvegatan 37, 223 62 Lund, Sweden

³Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94248, 1090 GE, Amsterdam, The Netherlands

Among the many unique flight behaviours of Common Swifts *Apus apus*, the most puzzling may be their ascents to high altitudes during both dusk and dawn. Twilight ascents have been hypothesized to be functionally related to information acquisition, including integration of celestial orientation cues, high-altitude visual landmarks and sampling of weather conditions. However, their exact purpose remains unknown. We tracked Common Swifts with tracking radar at their breeding grounds in southern Sweden, and present evidence that during the dusk ascent and dawn descent they often occur in flocks, whereas during the dusk descent and dawn ascent phase they do not. This flocking behaviour suggests that swifts may benefit from conspecific interactions during twilight ascents and descents, possibly through more robust cue acquisition and information exchange in groups, or extending social behaviour also seen in screaming parties before dusk.

Keywords: flight altitude, flight behaviour, screaming parties.

Rapid ascent or descent behaviour at twilight has been observed in a remarkable variety of vertebrates, from migratory fish (Willis *et al.* 2009) to raptors (Bouten *et al.* 2015) and swifts (Dokter *et al.* 2013). In all these species, such twilight behaviour has been hypothesized to play a role in challenges that require access to orientation cues; however, the precise function remains

unclear. In this study, we investigate the example of the Common Swift *Apus apus*. A full-year airborne lifestyle (Liechti *et al.* 2013, Hedenström *et al.* 2016), puzzling ascents to high altitude during twilight (Dokter *et al.* 2013, Meier *et al.* 2018) and conspicuous screaming parties during summer nights (Henningsson *et al.* 2010) are only a few of the remarkable behaviours exhibited by swifts (*Apus* spp.). The function of these remains highly elusive. Screaming parties of Common Swifts, where birds gather in flocks and perform rapid, acrobatic and highly vocal flight displays, are commonly observed during summer evenings (Lack 1956, Henningsson *et al.* 2010). The frequent interactions observed between individuals suggests this behaviour has a social component. Breeding birds usually spend the night on the nest, whereas non-breeders rapidly ascend to high altitudes (up to 3000 m) when the sun sets. Recent full-night monitoring of swifts' flight altitude at the breeding grounds by weather radar has revealed the characteristics of this twilight behaviour. After an initial rapid ascent, birds slowly decrease in altitude to spend the night flying at lower altitudes, only to increase altitude slowly soon before sunrise in a second ascent and then finally rapidly descend (Dokter *et al.* 2013). Flight altitudes thus change in close concert with changing light-levels, with the dusk ascent having approximate temporal mirror-symmetry to the dawn ascent. Signatures of twilight ascents have since been seen also in individual logging studies, showing that the behaviour is exhibited year-round at different locations and in multiple swift species (Liechti *et al.* 2013, Hedenström *et al.* 2016, Meier *et al.* 2018).

Before the discovery of the dawn ascent, hypotheses on the purpose of this behaviour centred on the bird's peculiar behaviour of sleeping while in flight. However, the occurrence of a second ascent at the end of the night makes it unlikely that the ascent represents the selection of a suitable flight altitude for sleep (Dokter *et al.* 2013), and ascents were also unrelated to selection of flight altitudes that minimize drift during roosting (Bäckman & Alerstam 2001). The finding that swifts seek high flight altitudes at the moment of twilight, and that similar flight altitudes are found at similar light levels at dusk and dawn (Dokter *et al.* 2013), suggests that the behaviour may involve a mechanism of light-level-dependent cue acquisition and integration (Dokter *et al.* 2013). The twilight period is exceptionally rich in orientation cues, such as star patterns and polarized light, whereas high flight altitudes increase the birds' perceptual range and access to visual landmarks, all important for orientation and navigation. Swifts could also use the ascents to assess surrounding weather conditions, including the altitudinal meteorological profile, while having optimal access to compass systems. This assessment could be critical for an aerial insectivore that is dependent on fair weather for foraging. Other

*Corresponding author.

Email: Cecilia.nilsson@cornell.edu

Twitter: @cnilsson709

suggestions have included nocturnal foraging (Buurma 2000), but the birds ascend well above nocturnal insect distributions (Dokter *et al.* 2013). Meier *et al.* (2018) suggested a social component of the behaviour of twilight ascents, by analogy with song in songbirds, which is also displayed primarily at dusk and dawn, and in connection with the behaviour of gathering in screaming parties at dusk. However, they were not able to test this with their individual logger data.

By tracking individual swifts and flocks of swifts by radar, we were able to track the degree of association in flocks by individuals across the full altitudinal range covered by the birds. Radar techniques are well-suited to identify flocking behaviour during night, when direct observations are not possible.

METHODS

We tracked Common Swifts (hereafter ‘Swifts’) with a tracking radar over six nights (24 June, 2, 8, 9 and 20 July, and 7 August) in the summer of 2013, and one night (16 July) in 2015. The radar was located in Lund, Sweden (55°42′50″N, 13°12′27″E, 91 m asl), and was operated from approximately sunset to sunrise on most tracking nights. Ground level in the study area varies between 20 and 70 m asl. The tracking radar used was an X-band radar (peak power 200 kW, pulse width 0.25 μ s, beam width 1.5°) which tracks individual targets, such as individual birds or tight flocks (Bäckman & Alerstam 2001). A single operator manually scanned the sky until a target (individual bird or flock) was identified, at which point the radar was locked to that target

and its exact position was automatically registered every second. From these positions, we calculated the ground-speed, vertical speed and flight altitude of the target.

Identifying birds to species is not possible with tracking radar, with the exception of Swifts, which have a characteristic wingbeat and flight pattern that make them easily distinguishable from other species (Bäckman & Alerstam 2001). When tracking flocks, however, wing beat frequencies of the individual birds are difficult to distinguish. At a typical tracking distance of 5 km, the pulse volume will be approximately 50 \times 130 m. Bird targets within that volume will not be distinguishable, but appear as one target, with a distinctly different wing beat signal than an individual target. This was used to identify flocks. In this study we have only included echoes that were clearly identified as individual Swifts, or flock echoes where the individuals at some point were far enough apart for us to be able to identify a Swift wing beat pattern. This usually occurred when one bird broke loose from the flock or the entire flock separated. It is not possible to assess flock size with this method.

The operators had no *a priori* expectations of differences in flocking behaviour during the night. The operator chose the altitude and direction to search for targets. Operators strived to sample all altitudes equally, but to avoid unintentional biases in altitudes sampled, as well as differences in overall flight altitude between nights (Dokter *et al.* 2013), we focused the analysis on altitude change (vertical speed; Fig. 1) rather than absolute heights. Due to ground clutter, the tracking radar cannot track targets below approximately 300 m and the highest altitude recorded in this study was 3702 m above

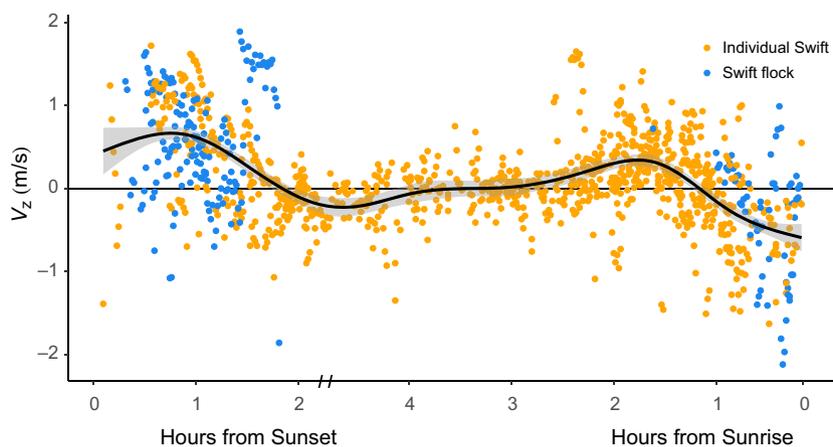


Figure 1. Vertical speeds V_z (m/s) of tracked Swifts. The mean of each 60-s period of the tracks is shown in relation to sunset or sunrise. Positive vertical speeds indicate increasing altitude (ascent) and negative vertical speeds indicate decreasing altitude (descent). Individual Swifts are in orange (total number of tracks = 209), and flocks of Swifts are in blue (total number of tracks = 29). The first part of the x-axis is labelled with hours after sunset, and the second part with hours before sunrise (cut at local midnight). The black line shows the smoothed mean of the vertical speed over time with the 95% confidence interval in grey (smoothing method: GAM, $V_z \sim s(\text{time}, \text{bs} = \text{'cs'}, k = 10)$).

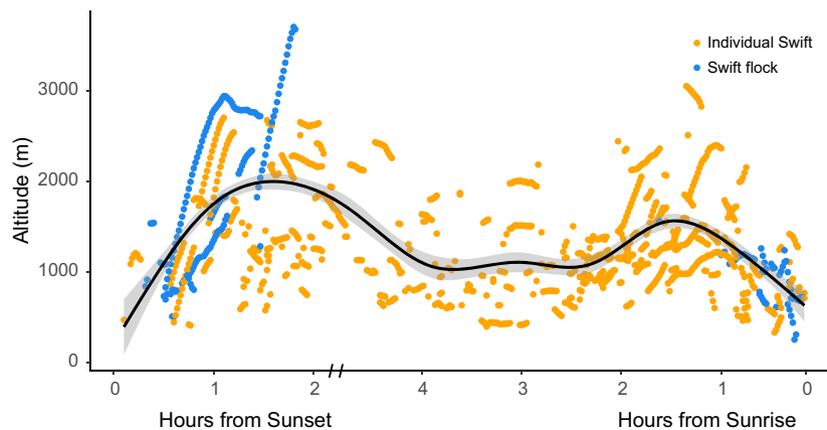


Figure 2. Altitude (metres above ground) of tracked Swifts. The mean of each 60-s period of the tracks is shown in relation to sunset or sunrise. Individual Swifts are in orange (total number of tracks = 209) and flocks of Swifts are in blue (total number of tracks = 29). The first part of the x-axis is labelled with hours after sunset, and the second part with hours before sunrise (cut at local midnight). The black line shows the smoothed mean of the vertical speed over time with the 95% confidence interval in grey (smoothing method: GAM, altitude \sim s(time, bs = 'cs'), $k = 10$).

ground. However, for completeness, and as supporting evidence, altitudes of all tracked targets are shown in Figure 2.

Targets were tracked for varying lengths of time, and tracks often included periods of level flight before or after an ascent/descent phase. We therefore divided tracks into 1-min intervals to be able to analyse the ascent/descent behaviour over the relevant time scale (Fig. 1). For each track interval, we calculated the number of minutes since sunset (if before midnight) or the minutes until sunrise (if after midnight) on that date, plotted together in Figure 1. We calculated a smoothed mean of all 1-min intervals using a generalized additive model (GAM) with cubic regression splines (formula: $y \sim s(x, \text{bs} = \text{'cs'}), k = 10$) in R, using ggplot2 (Wickham 2009). In total, we tracked 209 individual Swifts and 29 Swift flocks.

RESULTS AND DISCUSSION

Our data confirmed the expected pattern of two nightly ascents, one at dusk and one at dawn, with positive vertical speeds followed by negative vertical speeds. The two ascents displayed a similar temporal mirror symmetry between dusk and dawn as shown by Dokter *et al.* (2013). Figure 1 shows the vertical speed during different periods of the night. Soon after sunset, we observed a period of high vertical speeds, with most birds gaining altitude rapidly. This is followed by a period with negative vertical speeds, showing decreases in altitude, mostly with relatively modest vertical speeds. During the middle of the night, vertical speeds level out. About an hour before sunrise the birds start to gain altitude again, although not as rapidly as after sunset. Around

sunrise we see highly negative vertical speeds, as the birds rapidly decrease in altitude. The altitudes of tracked Swifts supported these patterns (Fig. 2).

From Figure 1, it is also apparent that the Swifts were aggregated in flocks predominantly during two periods of the night, during the dusk ascent and during the dawn descent, i.e. during the phases with relatively rapid vertical speeds (again, this pattern was supported by flight altitudes in Fig. 2). Interestingly, birds thus seemed to ascend in flocks in the evening, then descend individually and stay separated during the night until the morning descent, when birds were again observed in flocks. The flocking pattern followed the same temporal mirror symmetry as observed for the altitudinal patterns, in which the dawn ascent was a repetition of the dusk ascent, but with time progressing in reverse. No flocks were observed during the middle of the night.

These results offer the first concrete support of the theory that interactions between individuals may play a role in twilight ascents (Buurma 2000, Meier *et al.* 2018), but only during the rapid ascent (dusk) and decent (dawn) phases. During the phases when flocking was frequently observed, single flying Swifts were also detected, so flocking seems to be a common, but not necessarily essential, component of the ascent behaviour. During dawn descent, flocks were picked up mostly in the later descent phase. Therefore, flocks seem to form mostly during the descent, not at peak altitude. It is possible that the flocks we observed by radar at relatively high altitudes after sunset, climbing rapidly, correspond to the groups of birds engaged in screaming parties before sunset. However, anecdotal observations from the ground by the authors suggest that ascending flocks are considerably smaller than the screaming parties, which

can consist of over 50 birds. The period when no flocks were seen corresponds to the darkest period of the night, indicating that the Swifts might gather in flocks as soon as light levels allow them to see and identify conspecifics.

The range of vertical speeds measured here all fell well below the maximum vertical speeds measured in Swifts (Henningsson *et al.* 2010). This is not surprising as the twilight ascents consisted of longer, sustained flights rather than the short bursts of screaming flights. This makes it unlikely that the ascents are used as a challenge for signalling strength or vitality to conspecifics, which may be a component of screaming party behaviour (Henningsson *et al.* 2010).

Solving orientation, navigation and foraging challenges may benefit from social grouping. For example, a remarkable feature of migrating passerines performing dawn ascent is flock formation (Richardson 1978), which may be an expression of the Many Wrongs Principle (Simons 2004), the averaging of individual assessments during twilight reorientation to reach an optimal navigational decision. Assembling in groups might also improve assessments of local foraging opportunities and surrounding weather, including the sampling of the altitudinal meteorological profile during birds' rapid ascent and descent phases. This can be done through a central exchange of information, which can be based on simple inadvertent following behaviour (Bijleveld *et al.* 2010).

Meier *et al.* (2018) reported a higher frequency of twilight ascents in Alpine Swifts *Tachymarptis melba* in the African non-breeding period compared with migratory periods (a period assumed to require more orientation cues) and no change in frequency with shifting weather conditions. In their analyses, the probability of detection of an ascent depended directly on the altitude at twilight relative to the surrounding mean flight altitude, as well as the duration of the ascent (as it was sampled at 30-min intervals). Higher, longer ascents stand out more clearly relative to birds' mean flight altitude and were likely to have a higher probability of detection. During migration, ascents may be detected less often if birds fly in poorer weather conditions, leading to lower maximum ascent altitude (Dokter *et al.* 2013), and when birds migrate at already high altitudes, removing the need to ascend to even higher altitudes. The status of twilight ascents as a daily routine performed year-round, vs. an activity shown only under specific challenges, thus remains to be established.

Swifts' peculiar behaviour of sleeping on the wing exposes them to wind displacement during the night (Bäckman & Alerstam 2001). This could also increase their need of access to orientation cues during the non-migratory periods. Assessing their locations before, and particularly after, the night roosting flights could therefore require access to cues for reorienting, as well as for

assessing suitable locations for diurnal foraging. For this type of local navigation, access to visual landmarks from a high vantage point and assessment of local and surrounding weather might be particularly important. The need for reorientation after a night on the wing is supported by the finding by Meier *et al.* (2018) that Alpine Swifts were more likely to perform dawn ascents than dusk ascents (but note that such a difference was absent in Common Swifts on the breeding grounds; Dokter *et al.* 2013).

We conclude that there is preliminary evidence for association between birds in the rapid phases of twilight ascents, i.e. during dawn ascent and dusk descent. This lends the first support to the theory of a social dimension to this fascinating behaviour, which could be connected to the acquisition of orientation cues and collective weather profiling. However, the ultimate and proximate functions of twilight ascents remain unclear. Further studies are needed to investigate the role of flocking in the flight behaviour of Swifts, for instance by tagging large numbers of individuals with high-resolution altitude sensors to identify simultaneous ascent and descent behaviours.

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