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Drink safely: common swifts (*Apus apus*) dissipate mechanical energy to decrease flight speed before touch-and-go drinking

Swifts dissipate energy before drinking

Geoffrey Ruaux¹, Kyra Monmasson¹, Tyson L. Hedrick², Sophie Lumineau¹ and Emmanuel de Margerie¹

¹Univ Rennes, Normandie Univ, CNRS, EthoS (Éthologie animale et humaine) - UMR 6552, F-35000 Rennes, France.

²University of North Carolina at Chapel Hill, Chapel Hill, NC 27599, USA.

Corresponding author: Emmanuel de Margerie

e-mail: emmanuel.demargerie@univ-rennes1.fr

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Summary statement: This study shows that common swifts actively dissipate their mechanical energy before touching water when they drink in flight, possibly due to a trade-off between energy expenditures and safety.

Abstract

Flight is an efficient way of transport over a unit of distance, but it can be very costly over each unit of time, and reducing flight energy expenditures is a major selective pressure in birds. The common swift (*Apus apus*) is one of the most aerial bird species, performing most behaviours in flight: foraging, sleeping, and also drinking by regularly descending to various waterbodies and skimming over the surface. An energy-saving way to perform such touch-and-go drinking would be to strive to conserve mechanical energy, by transforming potential energy to kinetic energy during the gliding descent, touching water at high speed, and regaining height with minimal muscular work. Using 3D optical tracking, we recorded 163 swift drinking trajectories, over three waterbodies near Rennes, France. Contrarily to the energy conservation hypothesis, we show that swifts approaching a waterbody with a higher mechanical energy (higher height and/or speed 5 s before contact) do not reach water at higher speeds, but do brake, i.e. dissipate mechanical energy to lose both height and speed. Braking seemed to be linked with sharp turns and the use of headwind to some extent, but finer turns and postural adjustments, beyond the resolving power of our tracking data, could also be involved. We hypothesize that this surprisingly costly behaviour results from a trade-off between energy expenditure and safety, because approaching water surface requires fine motor control, and high speed increases the risk of falling into water, which would have serious energetic and survival costs for a swift.

Introduction

Flight is a locomotion mode which deeply influences the anatomy and behaviour of many bird species (Norberg, 1990; Podulka et al., 2004; Ruaux et al., 2020). In order to reduce energy expenditures associated with flight, birds have evolved a large diversity of anatomical and behavioural adaptations allowing them to reduce drag (e.g. feather structure; Chen et al., 2011; Feng et al., 2015; shape of wings; Tucker, 1993, 1995; or tail; Maybury and Rayner, 2001) or to extract energy from their environment (e.g. thermals; Cone, 1962; Shepard et al., 2011; or wind gradients; Warrick et al., 2016).

The common swift (*Apus apus*, hereafter “swift”) is a coursing insectivore with an extremely aerial way of life. Swifts can perform most of their behaviours in flight: foraging, mating and even sleeping (Lack and Owen, 1955; Lack, 1956; Bäckman and Alerstam, 2001, 2002; Gory, 2008). Some individuals were reported to stay airborne for 10 consecutive months (Hedenström et al., 2016), and swifts touch the ground almost only for egg laying and chick

rearing (Lack, 1951). For such an aerial species, flying at a low cost is an important adaptation. Flight behaviours in swifts have motivated numerous studies, whether it be in laboratories using wind tunnels with living specimens (Henningsson and Hedenström, 2011; Henningsson et al., 2014) or preserved wings (Lentink et al., 2007; Lentink and de Kat, 2014), or in the field with various tracking techniques (Bäckman and Alerstam, 2001; Henningsson et al., 2009, 2010; Hedenström and Åkesson, 2017; de Margerie et al., 2018; Hedrick et al., 2018), and swifts' abilities to reduce flight energy expenditures have been demonstrated in several contexts, but some of its flight behaviours have not been studied yet.

One of the few behaviours tying swifts to the Earth's surface is drinking. Due to their long, poorly retractable wings, swifts are unable to land to drink. It was reported that swifts are able to drink by swallowing rain drops (Bersot, 1931), but more generally they are often seen descending to waterbodies and gliding over them until they get close enough to open their beak and skim over the surface to get some water. This behaviour, while spectacular and not commonly observed amongst birds, has not been formally described yet.

In this study, we analysed swifts' drinking trajectories in order to determine if this behaviour fits within the general adaptation towards low-energy flight behaviours observed in this species. We digitized 3D trajectories of drinking swifts on three different waterbodies by using rotational stereo videography (RSV; de Margerie et al., 2015). Depending on the distance between the camera and the animal, this technique enables measurements of 3D trajectories with centimetric to metric spatial resolution, without the need to capture or tag animals (see Methods section and Fig. S1 for details on positioning error).

A first hypothesis would be that swifts minimize their energy expenditures and that they strive to conserve their mechanical energy during their gliding descent, converting potential energy to kinetic energy, thus reaching water surface at high speed. After contact with water, such kinetic energy would help the bird to regain height with less muscular work (i.e. flapping flight).

Alternatively, swifts may not conserve their energy as efficiently if they want to avoid reaching high speeds because of other constraints. Indeed, approaching and touching water surface at high speed must be demanding in terms of flight motor control, and increasing speed may reduce manoeuvrability (Wilson et al., 2015; Wynn et al., 2015). Additionally, destabilising forces generated by water contact will increase with the square of speed (Norberg, 1990). Hence, we assume that the risk of falling into water increases with flight speed. It is not reported in the literature whether falling into water would represent a significant survival risk for a common swift, but it certainly would cost the bird a considerable amount of energy to

escape from such an incident and leave the bird vulnerable to aquatic and terrestrial predators. Hence, aside from energy conservation, we also investigated possible braking methods (sharp turns, use of headwind) in order to understand if braking occurs and how it may occur.

Materials and Methods

List of symbols and abbreviations	
\mathbf{a}	acceleration vector in the ground reference frame
d	track direction in horizontal plane
d_w	wind direction in horizontal plane
d_d	angular difference between track direction and wind direction
E	mechanical energy (kinetic energy + potential energy)
E_k	kinetic energy
E_p	potential energy
g	magnitude of gravitational acceleration
L	resultant vector length for a set of d_d values
P	mass-specific kinematic power
r	instantaneous radius of curvature
RSV	rotational stereo-videography
s	bird speed in the ground reference frame
s_h	headwind speed
s_w	wind speed
\mathbf{v}	velocity vector in the ground reference frame
X	ground reference Cartesian position in the X direction, computed from smoothed inputs
Y	ground reference Cartesian position in the Y direction, computed from smoothed inputs
Z	ground reference Cartesian position in the Z direction, computed from smoothed inputs (height)
α	mean direction for a set of d_d values
Θ	azimuthal angle measurement from RSV
P	radial distance measurement from RSV
Φ	elevation angle measurement from RSV
ω	Rate of change in heading
\cdot	dot-over character, indicating first derivative with respect to time
$\ddot{}$	double dot-over character, indicating second derivative with respect to time
Subscript -5	variable calculated 5 s before water contact
Subscript 0	variable calculated at the instant of water contact
Subscript 1	variable calculated 1 second after water contact
Subscript 1s	variable averaged over 1 s
Subscript 5s	variable averaged over the entire 5 s descent

Recording sites and times

In order to understand the drinking behaviour of swifts across different landscape contexts, birds were recorded on three different waterbodies (hereafter site 1, 2 and 3). The three sites were located in Rennes Métropole, France. Site 1 was located on a segment of the Vilaine river (Fig. 1A, see also Fig. S2 for a ground view of the experimental setup). The river was around 70 m wide on this segment, and the RSV device was located on the south bank ($48^{\circ}06'34.3''\text{N}$ $1^{\circ}39'04.4''\text{W}$). Site 2 was located on a relatively small pond surrounded by trees from 6 to 9 m high (Fig. 1B). The longest distance between two banks was around 100 m, and the RSV device was located on the west bank ($48^{\circ}05'04.5''\text{N}$ $1^{\circ}37'59.8''\text{W}$). Site 3 was located on a wider pond surrounded by sparse trees from 10 to 20 m high (Fig. 1C). The greatest distance between two banks was around 170 m, and the RSV device was located on the east bank ($48^{\circ}06'54.0''\text{N}$ $1^{\circ}36'15.8''\text{W}$). The landscape surrounding the three sites was urban or suburban, with mainly buildings, roads, lawns and tree patches.

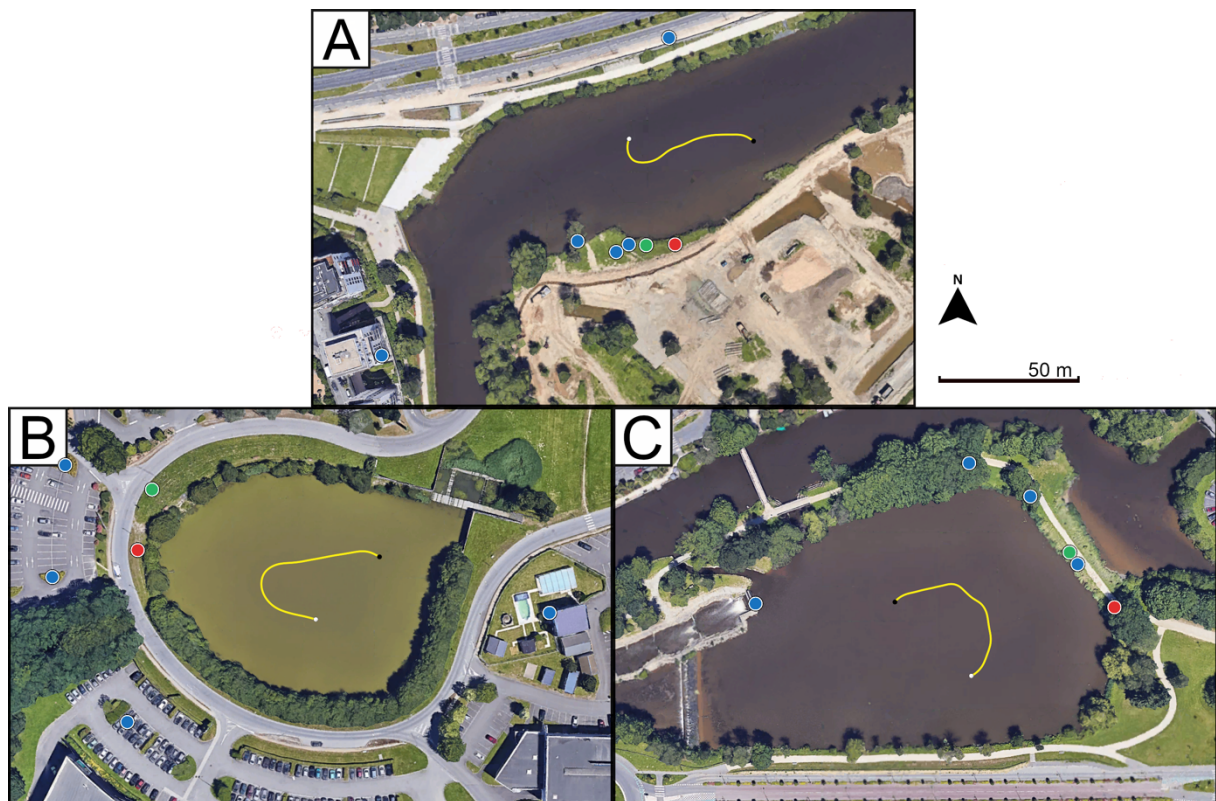


Figure 1: Aerial view of recording sites. (A) Site 1: river surrounded by open landscape. (B) Site 2: small pond surrounded by trees. (C) Site 3: large pond surrounded by sparse trees. The red dot indicates the RSV device, the green dot indicates the weather station, and blue dots indicate calibration points. The yellow lines show examples of swifts drinking trajectories, with the white dot marking the beginning of each track. Source for aerial view: Google Earth.

Recordings took place from May to July 2020, corresponding to the time when swifts are breeding in this region. 23 field sessions were carried out on this period, 7 on site 1, 8 on

site 2 and 8 on site 3. Recordings took place in the morning between 9:30 h and 12:00 h, when swifts were observed to be active over the three waterbodies during preliminary observations.

Rotational stereo-videography (RSV)

RSV is an optical tracking technique based on a set of mirrors projecting a stereo image of the animal on the sensor of a single camera (de Margerie et al., 2015). The analysis of the lateral shift between animal image pairs provides a measure of the distance to the animal. The rigid assembly of camera and mirrors can rotate horizontally and vertically on a tripod and fluid video head. While the operator rotates the device to keep the moving animal's image within the sensor frame, the aiming angles are recorded by angular encoders. The mathematical combination of distance, aiming angles and angular deviation from the optical axis yields a 3D record of the animal's movement.

We used an updated RSV device (Fig. S2) with a 1 m base length between the lateral mirrors, a Manfrotto 504HD fluid head (Cassola, Italy) equipped with 17-bit digital angular encoders (Kübler Sendix F3673, Villingen-Schwenningen, Germany), recording aiming angles at 200 Hz through an Arduino Mega microcontroller (www.arduino.cc) and an Adafruit Data logging shield (New York, USA). The device was equipped with a Panasonic DC-GH5S camera (Osaka, Japan) recording 4096×2160 -pixel frames at 60 Hz (150 Mbps H.264 compression) from a 19×10 mm sensor area, and a Nikon AF 105 mm f/2 lens (Tokyo, Japan), providing a 5.2° horizontal field of view. To get well exposed and sharp images, we used a 1/1300–1/640 s shutter speed and f/11 aperture, with ISO 1000–3200, depending on available light conditions. In order to help tracking the fast-flying birds, the camera was equipped with a Nikon DF-M1 dot sight viewfinder (Osaka, Japan).

Calibration and location error

The RSV distance measure, based on the lateral offset between left and right images of the bird, needs to be calibrated. For this purpose, we recorded four (site 2 and 3) or five (site 1) conspicuous targets on each site (signs, street lamps, structures on building roofs) located at fixed distances (20–143 m for site 1, 34–150 m for site 2, and 27–156 m for site 3). The real distance to these targets was measured with a Nikon Forestry Pro hand laser rangefinder (Tokyo, Japan).

The random positioning error was approximately 0.04 m at 25 m, 0.11 m at 50 m and 0.45 m at 100 m (Fig. S1).

Recording methods and wind measurements

During each 2.5 h field session, we attempted to record every individual swift approaching the waterbody (i.e. convenience sampling) and only retained recordings where the bird performed a descent towards water surface. In order to avoid pseudoreplication, we made sure to record a different individual after each drinking behaviour. Despite this precaution, pseudoreplication may be present to some extent in our data if (1) the same individuals came back at a drinking spot from a recording session to the next session and (2) if swifts performed several drinking behaviours during a given field session and were recorded several times. However, our field observations have shown that the three study sites were the main drinking location in each area, and that swifts were coming in successive “waves”, most probably from several colonies. Hence, we expect that pseudoreplication should be limited in our data, especially on site 1 and 2 where large numbers of swifts were regularly present (up to ~30 individuals simultaneously).

An initial total of 767 descending trajectories were recorded during our 23 field sessions. As some swifts occasionally glided over water without touching it, we only kept recordings where a contact with water was visible (foam at the water surface visible in the video frame). In order to analyse a sufficient and comparable portion of drinking trajectories, recordings starting less than 5 s before, or ending less than 1 s after water contact were removed. Moreover, recordings where the swift moved out of frame during more than 10 consecutive frames (i.e. more than 0.18 s missing at 60 Hz) were also removed. The resulting sample had 163 trajectories: 70 for site 1, 72 for site 2, and 21 for site 3, where swifts were less frequently observed. On each recording, the first frame on which the swift touched water was labelled, and all recordings were trimmed to keep 5 s before water contact, and 1 s after. Thus, each recording had a duration of 6 s at 60 Hz.

During each field session, a GILL Instruments MaxiMet GMX501 weather station (Lymington, UK) with ultrasonic anemometer was set up on a tripod, in order to measure the approximate wind speed and direction experienced by swifts approaching the waterbody. We placed the anemometer at 2 m height above the ground, as near as possible to the waterbody, and we also minimised proximity with any nearby tree. Wind speed and direction were recorded at 1 Hz, and were averaged over the 6 s of each trajectory.

Track processing

Stereo videos and angular records were processed with MATLAB r2018b (The Mathworks, Natick, MA, USA). To digitize the bird's locations in the video frames, the pixel at the centroid of the bird's body in the left half of each video frame was selected as the left point of interest (POI), either manually or with the help of semi-automatic tracking (DLTdv; Hedrick, 2008). Fully automated selection of left POI was initially tested, but appeared to be inefficient because of highly variable image backgrounds (sky, foliage, water). On the other hand, automated normalized cross-correlation between a 41×41 -pixel area around the left POI and the right image was used to find the corresponding right POI. Automated matching of right POI could also be misled by variable backgrounds, and thus was visually checked and manually corrected when needed. The bird's distance was then computed based on the site calibration reference.

RSV tracking yields spherical coordinates of the bird for each video frame (i.e. azimuth angle, elevation angle and distance from the device; Θ , Φ and P respectively). Raw coordinate series contain noise, due to (i) theoretical positioning uncertainty (increasing with P^2 , see de Margerie et al., 2015) and (ii) POI random positioning error in stereo images, which was exacerbated in the present study due to variable image backgrounds. Hence, we smoothed the raw spherical coordinate series using quintic splines, with an error tolerance based on the sum of (i) the per-point theoretical positioning uncertainty and (ii) the amplitude of high-frequency signal present in the coordinate series (as measured with 5 Hz filtering). These splines also interpolated short (≤ 10 frames) track bouts where the bird was out of frame (representing 408 positions out of 58843, i.e. 0.7 %). Smoothed spherical coordinates were then converted to cartesian coordinates (X , Y , Z) without additional smoothing. Similarly, smoothed cartesian speeds and accelerations (i.e. \dot{X} , \dot{Y} , \dot{Z} and \ddot{X} , \ddot{Y} , \ddot{Z}) were computed from the first and second derivatives of the spherical coordinate smoothing spline functions (Hedrick et al., 2018). An initial examination of smoothing results showed that high frequency noise was adequately removed from position series (i.e. >5 Hz movements were smoothed out, without signs of cut-off turns in the flight trajectory), but remained present in speed and acceleration data, an issue that could partly be improved by increasing the smoothing tolerance by 20 % (See details in Fig. S3). We also performed a sensitivity analysis, where the base smoothing tolerance was increased by 0% and 40%, with little effect on the results presented below (Table S1).

Biomechanical variables

In order to precisely describe and study drinking trajectories, a set of biomechanical variables was calculated. Firstly, to assess mechanical energy expenditure, the variables shown below were calculated.

Flight speed in the ground reference frame (m s^{-1}):

$$s = |\mathbf{v}| \quad (1)$$

where \mathbf{v} is the velocity vector ($\dot{X}, \dot{Y}, \dot{Z}$).

Mass-specific potential energy (J kg^{-1}):

$$E_p = gZ \quad (2)$$

Mass-specific kinetic energy (J kg^{-1}):

$$E_k = \frac{1}{2} s^2 \quad (3)$$

Mass-specific mechanical energy (J kg^{-1}):

$$E = E_p + E_k \quad (4)$$

Mass-specific kinematic power (W kg^{-1}):

$$P = \dot{E} \quad (5)$$

Note that energy and power values are mass-specific because the body masses of individual swifts are unknown.

In the following analyses involving mass-specific power, a guide value of -20 W kg^{-1} was used as a typical gliding power to illustrate our results. This value reflects the mass-specific power observed for swifts gliding at speeds around $13\text{--}16 \text{ m s}^{-1}$ (Hedrick et al., 2018). As expected from the glide polar curves estimates (Henningsson and Hedenström, 2011; Hedrick et al., 2018), swift gliding at lower or higher speeds will have slightly less or more negative power values (from ~ -10 to -30 W kg^{-1}), but power values much below this -20 W kg^{-1} standard would indicate fast energy dissipation, i.e. aerodynamically inefficient gliding.

Secondly, to measure flight turns in trajectories, we calculated the rate of change in heading (deg s^{-1}):

$$\omega = \frac{|\mathbf{v}|}{r} \quad (6)$$

where r is the instantaneous radius of curvature (m):

$$r = \frac{|\mathbf{v}|^3}{\sqrt{|\mathbf{v}|^2 |\mathbf{a}|^2 - (\mathbf{v} \cdot \mathbf{a})^2}} \quad (7)$$

where \mathbf{a} is the acceleration vector (\ddot{X} , \ddot{Y} , \ddot{Z}).

Note that r and ω measure flight direction changes in any plane, not limited to horizontal turns.

Finally, to test if wind speed and direction could influence drinking trajectories, the following variables were also calculated.

Track direction in the horizontal plane (deg):

$$d = \arctan(\dot{X}, \dot{Y}) \quad (8)$$

Angular difference between track direction and wind direction (deg):

$$d_d = d - d_w \quad (9)$$

Headwind speed (m s^{-1}):

$$s_h = s_w \cos(d_d) \quad (10)$$

It should be noted that track direction (d) designates the direction where the bird is heading, while wind direction (d_w) designates the direction from which the wind is coming. Hence, an angular difference of 0° is observed for a bird flying perfectly upwind (i.e. $s_h = s_w$), while a difference of 180° is observed for a bird flying perfectly downwind (i.e. $s_h = -s_w$).

Statistical analysis

All statistical analyses were performed in MATLAB r2018b. Linear models were created for each site to analyse the relationships between E_{-5} (mass-specific mechanical energy 5 seconds before water contact) and s_0 (speed at water contact), and between E_{-5} and P_{5s} (mass-specific kinematic power over the whole 5 s approach).

P was also calculated over each second before water contact (P_{1s}), yielding 5 power values for each trajectory. The distribution of these values for each site was visualised using violin plots created with the violinplot function in MATLAB (Bechtold, 2016), and the medians for each second were compared within each site using non-parametric Friedman tests (as the resulting distributions were not normal and not independent). Significant Friedman tests were followed by pairwise Wilcoxon tests with Bonferroni correction for 10 comparisons.

The link between ω_{1s} (mean rate of change in heading over 1 s) and P_{1s} was studied for each site using linear mixed-effects models with trajectory ID as a random effect.

Circular statistics were performed to analyse the distribution of the angular difference between track direction at water contact and wind direction (d_{d0}) using the CircStat toolbox in MATLAB (Berens, 2009). Mean direction (α) and resultant vector length (L) were calculated for all d_{d0} values on each site, along with a Rayleigh test for non-uniformity of

circular data (Fisher, 1993). Linear models were also created for each site to study the link between headwind speed (s_w) and the bird's speed at water contact (s_0).

Finally, to check for differences between the three sites, ANOVA were carried out to compare Z_{-5} , Z_1 , s_{-5} , s_0 , and s_1 . Significant ANOVA were followed by Tukey-Kramer post hoc tests.

Results

General description of drinking trajectories

Figure 2 shows average patterns of height (Fig. 2A–C), speed (Fig. 2D–F) and mass-specific mechanical energy (Fig. 2G–I) variations through time in our 3 study sites. Flight trajectories were variable within each site (as shown by the large standard deviations), and some tendencies also differed between sites. Differences between waterbodies will be discussed later and here we firstly focus on congruent aspects that help understand the general drinking behaviour of swifts.

Five s before water contact, swifts were flying at a mean height of 9.3, 11.6 and 12.7 m (for site 1–3 respectively) and were descending towards water surface. As expected from energy conservation principle, the ground speed of swifts initially increased as they were losing height, from approximately 12 m s^{-1} up to 13.0, 13.7 or 14.6 m s^{-1} depending on site. However, starting around -1.5 s , mean speed decreased to 11.0, 12.2 and 11.9 m s^{-1} at water contact. Such deceleration, happening while birds were still losing height was not consistent with a basic hypothesis of energy conservation, and suggested that braking may have occurred before water contact.

Note that the average mechanical energy, summing potential and kinetic energy, was decreasing during descent (Fig. 2G–I) because swifts were gliding during most of their approach, and any gliding bird loses energy due to drag. However, the energy slope (i.e. power) became more negative as time passed, suggesting energy was dissipated more rapidly as the birds approached water. Following water contact, mechanical energy increased as the birds flapped their wings to regain height.

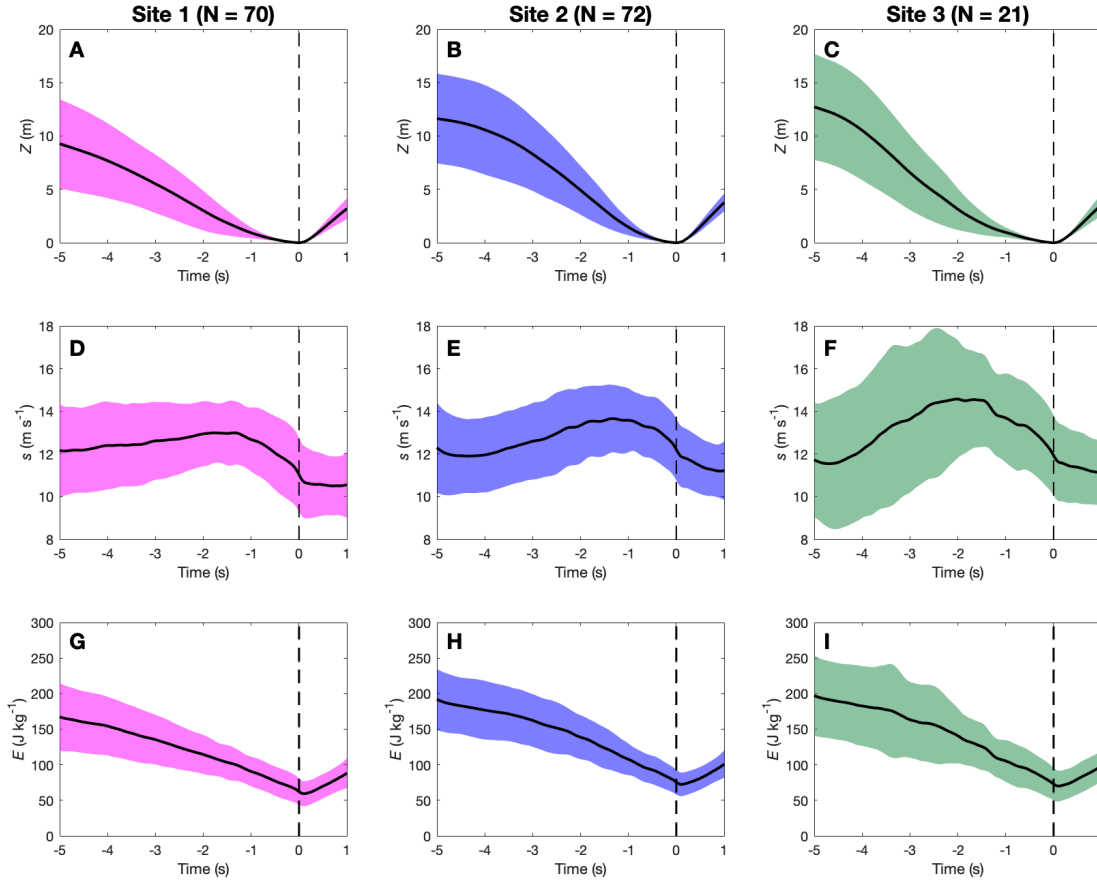


Figure 2: Mean height (Z), ground speed (s) and mass-specific mechanical energy (E) versus time to water contact on each site. The coloured zones represent ± 1 SD. The vertical dashed lines show the time of water contact ($t = 0$). Site 1: $N = 70$, site 2: $N = 72$, site 3: $N = 21$.

Energy conservation vs. dissipation

A more specific approach to test for energy conservation was based on the observed within-site variability of biomechanical variables during approaches. If swifts strived to conserve their mechanical energy, birds that had a higher energy level 5 s before water contact (higher height and/or higher speed at -5 s) should have touched water at a higher speed, once potential energy has been converted to kinetic energy. Contrarily to this prediction, there was no significant relationship between E_{-5} and s_0 , in any of the 3 sites (Fig. 3A–C). This means that the speed of swifts at water contact was independent from their mechanical energy 5 s earlier, which would not be expected if swifts did conserve their energy. Conversely, there was a very significant relationship between E_{-5} and P_{5s} (Fig. 3D–F), showing that swifts that had more mechanical energy 5 s before water contact did not try to save this energy (by transforming E_p into E_k), but rather dissipated excess energy during descent, by generating a more negative power. This result demonstrates that swifts do brake, in proportion to their mechanical energy 5 s before water contact. Note that here we use the verb “brake” in an “air-brake” sense, i.e.

decreasing lift/drag ratio, which can result in decreasing speed and/or losing height (Norberg, 1990).

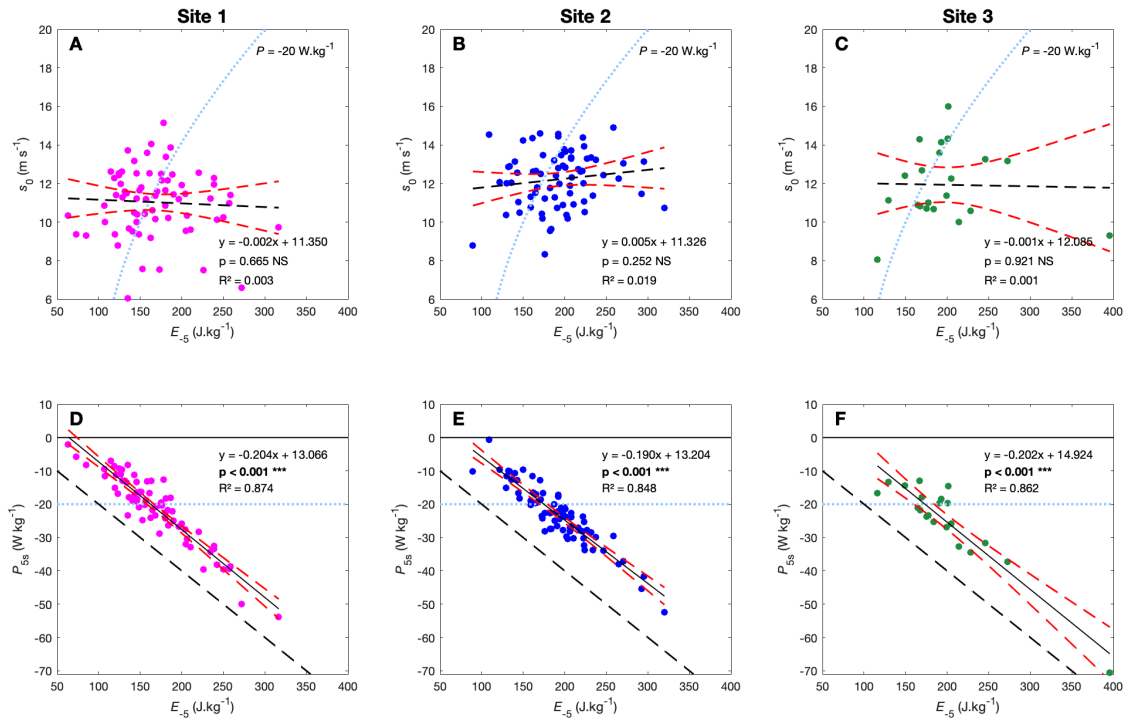


Figure 3: Speed at water contact (s_0) and kinematic power over 5 s (P_{5s}) versus mechanical energy 5 s before water contact (E_{-5}). Each linear model, p-value and R^2 are indicated in each panel. The red dashed lines represent the 95% CI of the slope. The blue dotted line represents the expected relationships for energy conservation, minus a -20 W.kg^{-1} kinematic power, a typical value for a gliding swift. The black dashed line (D–F) represents the relationship which would be observed for a swift dissipating all its mechanical energy during the 5 s approach. Site 1: $N = 70$, site 2: $N = 72$, site 3: $N = 21$.

Investigation of energy dissipation patterns

In order to better understand how swifts braked, we first looked at the variations of dissipative power through time. As explained in the methods section, smoothed speed data still contained some noise, which prevented us from computing reliable instantaneous power values. As a second-best option, we relied on power values computed from energy gain/loss over 1 s intervals (P_{1s} , Fig. 4A–C). A feature common to all sites is that energy dissipation was stronger during the last second before water contact (median $P_{1s} = -27$, -30 and -29 W.kg^{-1} on site 1, 2 and 3 respectively, compared to -12 , -13 and -13 W.kg^{-1} between -5 and -4 s). On site 1 and site 2 (Fig. 4A and 4B), power was also significantly more negative between -2 and -1 s before water contact than earlier in the approach. In other words, P_{1s} was close or above the typical value of -20 W.kg^{-1} at the beginning of the recorded approach, indicating efficient

gliding and conversion of potential energy to kinetic energy, but fell below -20 W kg^{-1} near the end of the descent on all sites. Thus, braking seems to occur mainly in the last portion of the approach, which is consistent with the speed curves showing a deceleration about 1.5 s before water contact (Fig. 2D–F). Note that P_{1s} was sometimes positive, which reflected portions of trajectories where some flapping occurred. Also note that, as expected, P_{1s} values were particularly high during the second following water contact (not presented here) when birds continuously and vigorously flap their wings to regain height (medians of +25, +25 and +28 W kg^{-1} respectively).

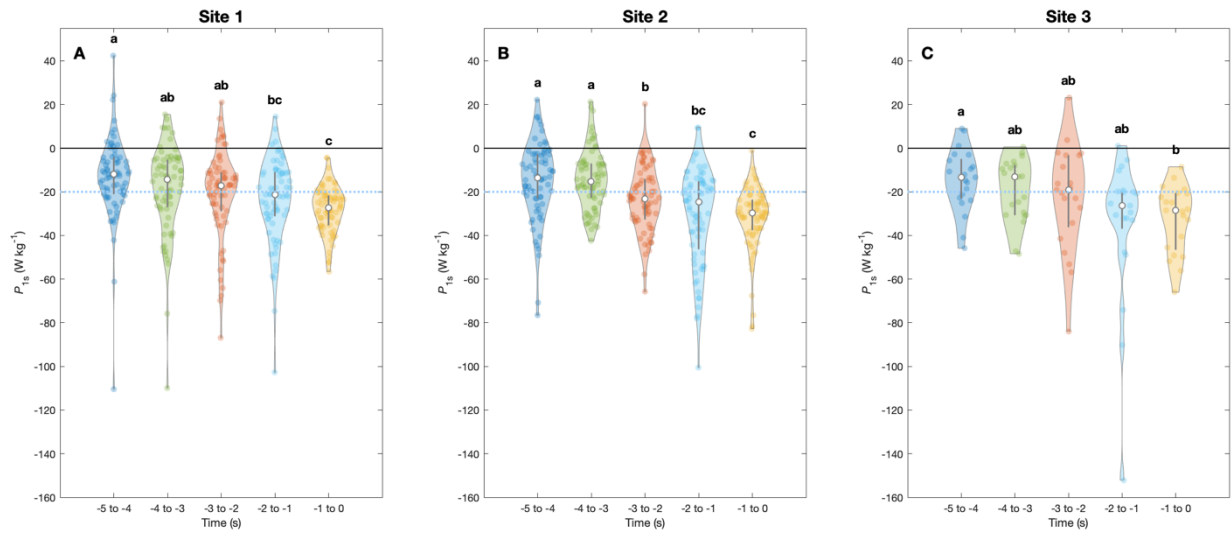


Figure 4: Distribution of kinematic power (P_{1s}) versus time to water contact. White dots represent the medians, vertical bars represent the 25th to 75th percentile ranges, and coloured zones represent the kernel density distributions of each category. Lowercase letters (a, b and c) indicate significant differences (Friedman test followed by pairwise Wilcoxon tests with Bonferroni correction for 10 comparisons). The blue dotted line indicates a kinematic power value of -20 W kg^{-1} . Site 1: $N = 350$ (from 70 trajectories), site 2: $N = 360$ (from 72 trajectories), site 3: $N = 105$ (from 21 trajectories).

Another interesting question was whether energy dissipation was linked to turning behaviours of birds approaching water. An aerial view of all trajectories showed the great diversity of approaches during the 5 s before water contact (Fig. S5). Overall, sinuous trajectories were the rule, and a few direct approaches were only seen on site 1 and site 3, as expected for a river and a wide pond offering a greater freedom of approach. Prolonged turns could be seen in most trajectories, and all of them converged to a straight line before water contact.

In Fig. 5, we studied the relationship between turning (measured through mean 3D rate of change in heading, ω_{1s}) and P_{1s} , both averaged over 1 s intervals. Results suggest that swifts did not use a single strategy to brake, and that turning was not necessarily a cause of energy dissipation. Indeed, even though a significant negative relationship could be observed on site 1

(Fig. 5A), suggesting that swifts braked more during sharp turns, the explanatory power remained weak ($R^2 = 0.086$). Moreover, the relationship was not significant on site 2 and site 3 (Fig. 5B and 5C). The wide scattering of power values on each panel revealed that, even if braking during sharp turns was visible on some portions of trajectories (strongly negative P_{1s} values for high ω_{1s} values), other portions also showed strong braking without sharp turns (strongly negative P_{1s} values for low to intermediate ω_{1s} values), or even sharp turns without braking (high ω_{1s} values with P_{1s} close to -20 W kg^{-1}). Overall, this great dispersion suggests a wide diversity of strategies used by swifts when approaching water, and sharp turns alone cannot explain all braking events. And indeed, if the timing of braking (Fig. 4) is compared with the aerial view of trajectories (Fig. S5), it appears that the portion of trajectories where the strongest braking occurs (the last second) may actually be close to a straight line for many trajectories.

Note that averaging power and rate of change in heading over 1 s was limiting here, as very short turning manoeuvres (and the possibly associated energy dissipation bursts) could remain unnoticed. Careful frame-by-frame observation of individual trajectories (e.g. Movies 1–3) suggested that braking might indeed rely on a variety of postural changes (including alternating banking, wing dihedral, high incidence of body or tail, and even leg trailing), that happened at a much shorter timescale, and not necessarily associated with strong, prolonged heading change.

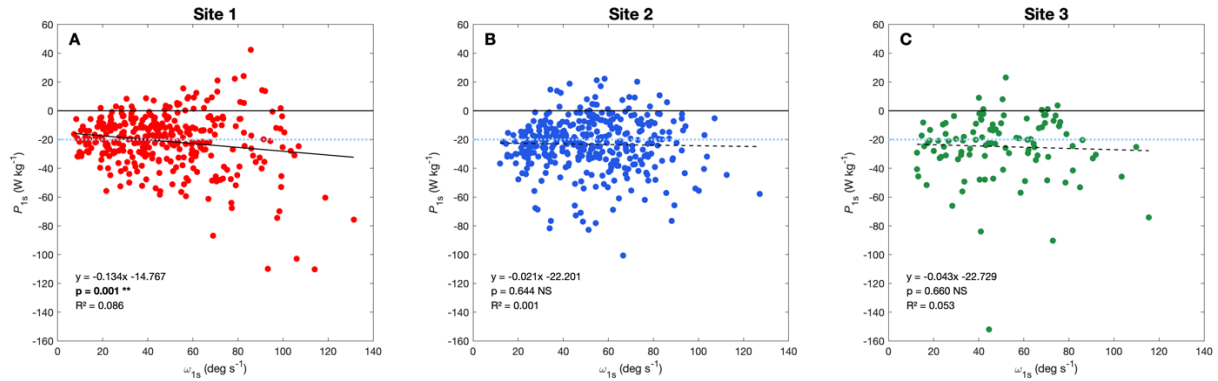


Figure 5: Kinematic power (P_{1s}) versus rate of change in heading (ω_{1s}). Each point represents a mean value over a period of 1 s during the approach to water. Each trajectory thus has 5 data points. Each linear mixed-effects model, p-value and R^2 are indicated in each panel. The blue dotted line indicates a kinematic power value of -20 W kg^{-1} . Site 1: $N = 350$ (from 70 trajectories), site 2: $N = 360$ (from 72 trajectories), site 3: $N = 105$ (from 21 trajectories).

A third question regarding braking behaviour was whether swifts used wind to help them lower their kinetic energy in the ground reference frame before water contact. Although we did not experience strong winds (maximum of 3.9 m s^{-1}), and most of our field sessions occurred on days of weak wind ($< 2 \text{ m s}^{-1}$ for 90% of trajectories), we tested whether swift

preferred to drink in an upwind direction, as this strategy could help them to lower their ground speed, while preserving their airspeed. Angular differences between track direction at water contact and wind direction showed a strongly skewed distribution (Fig. 6). On all sites, most swifts preferentially touched water while flying upwind, and tailwind was rarely observed. Note that as our anemometer was not placed exactly at the point of water contact, but necessarily at some distance, on the water bank, differences between wind experienced by the birds and measured wind exist, and might account for some of the dispersion observed in Fig. 6.

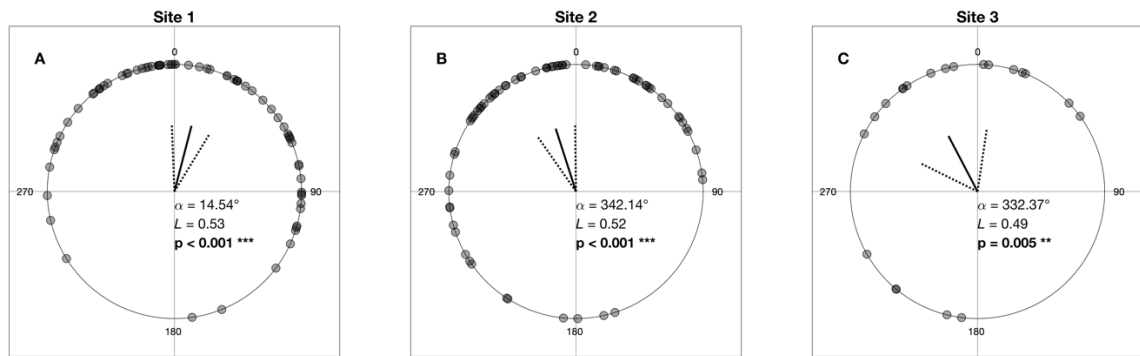


Figure 6: Angular difference (α) between track direction at water contact and wind direction. A value of 0° is observed for a bird flying perfectly upwind. Mean angles (α) and vector lengths (L) are given together with p-values for departure from random circular distributions (Rayleigh test). Dotted lines represent the 95% CI. Site 1: $N = 70$, site 2: $N = 72$, site 3: $N = 21$.

A more detailed understanding of how swifts used wind was obtained from the relationship between bird ground speed at water contact (s_0) and headwind speed (s_h , Fig. 7). These two variables showed a significant relationship on site 1 (Fig. 7A), with an intermediary slope of -0.7, which suggested that swifts might have used headwind to lower the ground speed of water contact (-1 slope, black dash-dotted line), but also partly to brake less (0 slope), increasing airspeed by a small amount and saving some energy. Note that negative s_h (i.e. tailwind drinking) was rare and mainly observed at low wind speeds. In site 2 and 3, the relationship was not significant, but the slopes were also between -1 and 0. It is worth noting that wind speed values superior to 2 m s^{-1} were only rarely encountered outside of site 1, which could make it more difficult to detect a relationship on site 2 and site 3.

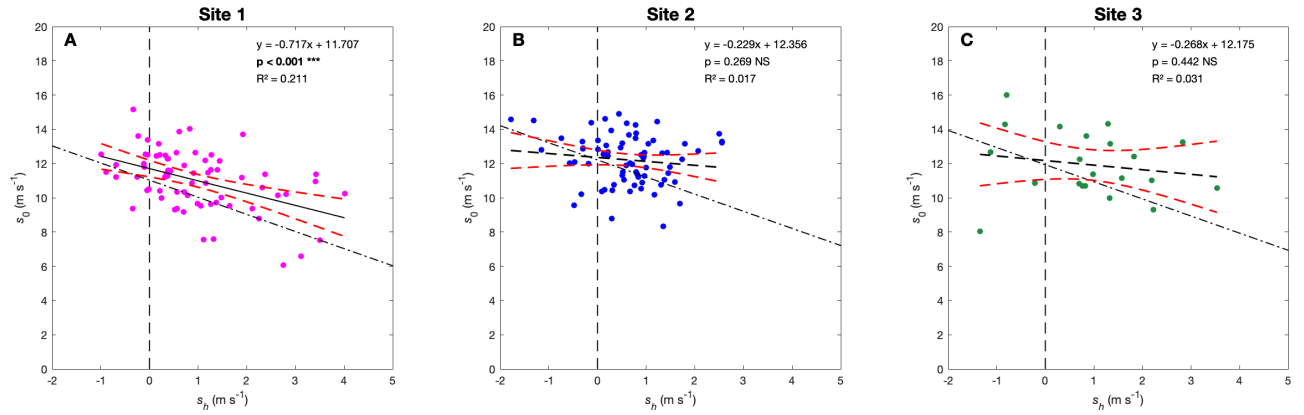


Figure 7: Ground speed at water contact (s_0) versus headwind speed (s_h). Each linear model, p-value and R^2 are indicated in each panel. The red dashed lines represent the 95% CI of the slope. The black dash-dotted line represents the equation $y = \bar{y} - x$ (where \bar{y} is the mean over the whole distribution) which would be expected if swifts maintained the same airspeed irrespective of wind. Site 1: $N = 70$, site 2: $N = 72$, site 3: $N = 21$.

Additional influences of local landscape

Finally, even if congruent general tendencies could be observed in swifts' drinking behaviour across the three study sites, some differences were still present. ANOVA followed by Tukey-Kramer tests (Table 1) showed that average height 5 s before contact (Z_{-5}) was significantly lower on site 1 compared to the other sites. Other significant differences could be detected between site 1 and site 2: the average speed at which swifts touched water (s_0) was lower, and average speed (s_1) and height (Z_1) 1 s after water contact were lower on site 1 compared to site 2.

The fact that swifts flew, on average, at a lower height 5 s before, and 1 s after contact on site 1 could be linked to the more open landscape surrounding this river and the absence of high trees (see Fig. 1), offering a greater freedom to approach water and climb back.

Also observed on site 1 was a lower speed at water contact. The difference with site 2 amounted to 1.18 m s^{-1} for s_0 in Table 1 (reduced to 0.65 m s^{-1} when there was no headwind, i.e. intercept values in Fig. 7A–B). Swifts approaching the waterbody at a lower height would gain less speed during descent and would thus need to brake less to keep their speed in their preferred range. However, as this lower height observed on site 1 was also associated with a lower speed at water contact, this suggests that swifts drinking on site 1 did not necessarily take advantage of this open landscape to brake less, but rather prioritised safety, by drinking at a slightly lower speed on average.

These differences across drinking sites suggest that landscape, by constraining the height of approach and the space available to climb back, might shift the local ideal drinking

speed, i.e. the flight speed that balances energetic cost (braking during descent implies work during subsequent climb, and a steeper climb requires greater muscle power) and the risks of high-speed water contact. In other words, waterbodies surrounded by tall trees (sites 2 and 3), requiring a steep climb after water contact, would urge swifts to brake less and to favour slightly higher, less safe water contact speeds.

Table 1: Results of ANOVA followed by Tukey-Kramer *post-hoc* tests comparing speed and height variables at -5 s, 0 s, and 1 s between the three sites. Mean \pm SD. Site 1: N = 70, site 2: N = 72, site 3: N = 21.

Variable	Site 1	Site 2	Site 3	ANOVA (p)	Tukey-Kramer (p)
Z_{-5} (m)	9.29 ± 4.21	11.64 ± 4.23	12.73 ± 5.11	< 0.001 (***)	1:2 (0.004) / 1:3 (0.004) / 2:3 (0.57)
Z_1 (m)	3.19 ± 0.97	3.77 ± 0.83	3.56 ± 1.03	0.001 (**)	1:2 (<0.001) / 1:3 (0.25) / 2:3 (0.63)
s_{-5} (m s ⁻¹)	12.17 ± 2.19	12.30 ± 2.14	11.74 ± 2.76	0.598	
s_0 (m s ⁻¹)	11.03 ± 1.73	12.21 ± 1.46	11.93 ± 1.93	< 0.001 (***)	1:2 (<0.001) / 1:3 (0.07) / 2:3 (0.77)
s_1 (m s ⁻¹)	10.56 ± 1.56	11.22 ± 1.39	11.15 ± 1.56	0.025 (*)	1:2 (0.02) / 1:3 (0.25) / 2:3 (0.98)

Discussion

Our study is the first quantitative and spatial description of the drinking behaviour of the common swift, and our dataset provides an opportunity to test hypotheses related to energy conservation. Our results showed that swifts did not prioritise mechanical energy conservation when they approached water. Indeed, for a given water body, swifts having a higher mechanical energy 5 s before water contact did not reach water at higher speeds (Fig. 3A–C) but braked more strongly (Fig. 3D–F). Mechanical energy dissipation was especially strong during the last seconds (Fig. 4), and as a result, average speed showed a marked decrease during the last 1–2 s (Fig. 2D–F). On top of this general drinking behaviour, consistent across the three study sites, local landscape structure influenced drinking trajectories to some extent (Table 1), since a more open landscape seemed to allow swifts to approach water at lower heights and to drink at lower speeds.

If swifts converted potential energy to kinetic energy, only losing energy at a rate of about -20 W kg^{-1} while gliding, points in Fig. 3 would scatter along blue dotted lines. Most notably, speed at water contact (s_0) should increase steeply with E_{-5} (Fig. 3A–C), exceeding 20 m s^{-1} for the birds approaching the waterbody from the highest observed height and speed at -5 s . This was not what we observed, with birds drinking water at $11.7 \pm 1.7 \text{ m s}^{-1}$ (mean \pm SD for all sites), irrespective of energy level 5 s before drinking. To achieve this, swifts reduced

mechanical energy at rates as negative as -50 or even -70 W kg^{-1} (averaged over 5 s), several times the power observed during typical gliding.

On each site, the observed relationship between P_{5s} and E_{-5} was almost parallel to the black dashed line in Fig. 3 D-F, representing the relationship which would be observed if swifts dissipated all their mechanical energy during descent ($P_{5s} = -0.2 E_{-5}$). The observed slopes were all close to -0.2 , but the intercept was not 0. The intercept value represents the energy that swifts have to save, despite dissipating all other extra energy, in order to reach their preferred range of s_0 . For example, in site 1, an intercept of 13 W kg^{-1} higher than a trajectory dissipating all of its energy indicates that over 5 s, the bird keeps 65 J kg^{-1} over the descent, translating into 11.4 m s^{-1} at water contact (see equation 3), which falls right in the middle of the observed range of s_0 values in site 1 (Fig. 3A).

It is also worth noting that some trajectories showed a P_{5s} value superior to the typical gliding value of -20 W kg^{-1} (Fig. 3D-F), which reflects that slow gliding flight (nearer to the minimum sink rate speed, dissipating around -10 W kg^{-1} , Hedrick et al. 2018) or even short bouts of flapping flight ($P > 0$) were involved in these cases. This was mostly observed for trajectories with a value of E_{-5} lower than 175 J kg^{-1} . A swift with this amount of mechanical energy gliding according to the reference value would dissipate 100 J kg^{-1} during the descent (-20 W kg^{-1} over 5 s), thus reaching $E_0 = 75 \text{ J kg}^{-1}$, which is close to the preferred range discussed above. Hence, swifts having a value of E_{-5} even lower than 175 J kg^{-1} (because they approached the waterbody at low height or were flying slowly) probably had to flap at some point of their approach in order to keep s_0 in their preferred speed range.

How do swifts dissipate their mechanical energy?

Our results show that swifts dissipated mechanical energy during descent, but the underlying methods of braking (i.e. increasing drag during the last moments before water contact, and also possibly reducing lift earlier in the descent) were not completely understood. Braking with sharp turns was used to some extent, but did not constitute the full picture (Fig. 5). A more general way for swifts to control lift/drag ratio is to modify the angle of attack and shape of various parts of their flight apparatus (wings, tail, body) while gliding (Norberg, 1990; Lentink et al., 2007; Henningsson and Hedenström, 2011), and we qualitatively observed examples of such postural change in our video records (Movies 1–3). Some of these braking manoeuvres implied alternating banking (see e.g. Movie 3) that might be similar to

“sideslipping” described in bats (Norberg, 1976). Moreover, leg trailing was sometimes observed in our video records before water contact (Movie 3) and could be another way to increase drag as shown in other birds by Pennycuik (1968, 1971). It is also probable that the wide opening of the beak before water contact increases drag to some extent.

Describing braking (both postural changes and the associated energy dissipation) at a very fine temporal scale is beyond the reach of our approach. Due to the amount of noise in our trajectometry data, power and rate of change in heading were averaged over intervals of 1 s, and very short manoeuvres may have been overlooked. Moreover, in our study, swifts were considered as a point in 3D space, and RSV spatial resolution (median random positioning error of ~0.15 m) is not sufficient to study the effect of different body parts on braking. Future studies could consider looking more precisely at the kinematics of each body part in order to better understand braking techniques.

In addition to braking techniques, we showed that swifts preferentially drank in an upwind direction (Fig. 6). Flying upwind is a way to reduce swifts’ ground speed, and it seems that headwind can be used to reduce their need to brake, at least to some extent (Fig. 7). However, it is worth noting that the wind speeds measured by our weather station 2 m above the waterbody bank, differed from the wind speeds encountered by a swift flying close to the water surface because of the wind gradient in the boundary layer (Ruggles, 1970; Warrick et al., 2016). When a bird flying into headwind is losing altitude, headwind speed should gradually decrease, and hence the ground speed of the bird should increase, which calls for more braking. Consequently, headwind should be less useful for the birds to brake in the last meters before touching water. Studying the exact contribution of wind gradient to drinking flight behaviour would require more refined wind measurements than what we recorded for the present study, i.e. horizontally closer to the water contact position, and at several heights above water.

Additionally, ground effect, which can be defined as a reduction of induced drag when flying close to a surface, must also have some influence on drinking swifts approaching water. This effect is considered to be significant when a bird flies at a height below half of its wingspan (Norberg, 1990), which would be around 24 cm for a swift with a wingspan of 48 cm (Chantler et al., 2020). Thus, the drinking flight of swifts is most probably influenced to some extent by this reduction of drag during the last second before water contact, which would call for even more braking.

Trade-off between flight performance and safety

Even if the common swift is known for its various aerodynamic and energy-saving behaviours, mechanical energy can be dissipated to a great extent while approaching water. We estimated power values as negative as -70 W kg^{-1} when averaged over 5 s, and down to -190 W kg^{-1} during isolated braking manoeuvres (Movie 2). These rates were much more negative than the approximately -20 W kg^{-1} typical gliding power at similar speeds (Hedrick et al., 2018). As a result, swifts had to output a greater amount of muscular energy after drinking to regain altitude with flapping flight (which occurred at a rate around $+25 \text{ W kg}^{-1}$). The main hypothesis to explain this counter-intuitive waste of energy during descent to the water body is that, in this case, other constraints might be more important for the swift than reducing energy expenditure. Touching water at very high speeds could be a danger for a drinking swift, because the contact would be more violent. Indeed, the drag force induced by water increases with the square of speed (Norberg, 1990), quickly increasing the risk of destabilisation (hydrodynamic drag on the bird's lower beak is not applied along the body axis). The bird's beak should penetrate water with a depth of only a few millimetres, and a very fine motor control and manoeuvrability are necessary for this behaviour. Moreover, as swifts approach water surface, flapping their long wings becomes more and more difficult, so they have to rely on postural adjustments while gliding. It is generally considered that such very fine control is more difficult to achieve at higher speeds (Wilson et al., 2015; Wynn et al., 2015). Additionally, violent contact with water could potentially cause damage to the jaw or jaw muscles of a swift.

These results suggest that swifts may have a preferred range for their speed at water contact, braking when they approach water too quickly, and actively flapping when they approach it too slowly (keeping speed higher than stall speed is another constraint). Slower flight speeds presumably decrease the risk of falling into the water, but only up to a point. Slower flight speeds are also a challenge for gliding birds, because the sinking speed increases, and stalling may occur at the slowest speeds (Norberg, 1990). Hence, a “preferred speed range” seems to exist for drinking swifts. This observation is consistent with the “speed-choice” framework proposed by Wilson et al. (2015), which states that animals choose specific speeds for specific behaviours depending on biomechanical trade-offs between speed and various factors such as energetic constraints, manoeuvrability, and motor control. Mistakes can have varying energetic or even survival costs depending on the behaviour, and the consequences of any inaccurate movement (wasted energy, injury, death) can deeply influence this trade-off. In

the case of drinking swifts, mistakes could result in a fall into water. Even if it is rarely observed and, to our knowledge, not reported in the literature on common swift, we can hypothesize that falling into water would be an important survival risk and energetic cost for a swift, because it would not be able to take flight easily. Brunton (2019) reported an observation of a white-throated swift (*Aeronautes saxatilis*) that had fallen into a lake. The bird vigorously swam for 10 minutes, synchronously stroking its long and narrow wings, before reaching the lakeshore, approximately 85 m away. Its body feathers were soaked and it remained inactive for 45 minutes. The observers then decided to keep it overnight in a cardboard box, and the stranded bird successfully took flight in the following morning, showing that it was apparently not injured. Similar swimming behaviours were also reported in the barn swallow (*Hirundo rustica*; Jackson, 1970; Brown and Brown, 2020), the tree swallow (*Tachycineta bicolor*; Winkler et al., 2020), the cliff swallow (*Petrochelidon pyrrhonota*; Brown et al., 2020), and the bank swallow (*Riparia riparia*; Garrison and Turner, 2020). From these observations, we can hypothesize that such an incident would involve similar consequences for a common swift, which would be associated with large energy expenditures and a long period of vulnerability to predators. Thus, a trade-off seems to exist between lower energy expenditure in flight and higher safety in close proximity of the ground, and this trade-off can be shifted by environmental conditions such as wind or landscape structure.

It is worthwhile to note that, during field sessions, some swifts were sometimes seen approaching water surface in a typical way similar to a drinking behaviour, but glided close to the surface without touching it, regaining height and sometimes performing another descent right after. This behaviour could be considered as an “aborted” drinking behaviour where, for some reason (lack of balance, excessive speed, proximity of other individuals or of landscape elements), the individual decided to regain height without taking the risk to touch water. If these behaviours really are aborted attempts, they show that swifts sometimes prefer sacrificing a large amount of energy by regaining height and performing another approach, rather than touching water in a risky situation.

A risky but essential behaviour

Even if the common swift is extremely adapted to an aerial lifestyle (Lack, 1956; Bäckman and Alerstam, 2001), and is often considered to be tied to Earth only during the breeding period (Lack, 1951; Hedenström et al., 2016), a regular contact with the Earth’s surface for drinking still constrains its way of life. Taking into account the fact that flying close

to the ground in relatively cluttered environments might represent an increased collision risk for such an aerial species, and adding potential survival and energetic costs of falling into water, water intake probably represents an important motivation. Insectivorous birds are predicted to obtain sufficient water from their invertebrate prey (Bartholomew and Cade, 1963), and are consequently rarely observed drinking at waterbodies, even in arid environments (Lee et al., 2017). Swallows and swifts represent notable exceptions to this trend and often drink surface water, and one explanation could be that these very aerial birds lose more water by evaporation than more terrestrial birds due to their greater energy expenditure in flight (Salt and Zeuthen, 1960; Bartholomew and Cade, 1963). This hypothesis is also consistent with observations that swifts strive to retain water and limit evaporation, by prioritizing non-evaporative cooling (leg trailing) over evaporative cooling (gaping), the latter being very rarely observed even in hot weather (Neumann, 2016). Thus, even if swifts are able to obtain water from rain drops (Bersot, 1931), from nestlings faecal sacs (Dell’Omo et al., 1998), and probably from invertebrate prey (Bartholomew and Cade, 1963), their water needs still seem high enough to motivate them to perform this unique drinking behaviour over various waterbodies.

To conclude, our study describes an energetically suboptimal behaviour in the common swift, possibly due to a trade-off between energy expenditures and safety. When they have to drink, fast-flying swifts brake before water contact, probably to reduce the risk of touching water at speeds too demanding for their motor control skills, which could cause a fall into water or mechanical damage. It is a well-known fact that birds regularly brake and dissipate some mechanical energy when interrupting their flight for landing or perching (Norberg, 1990). Although common swifts are known as “continuous fliers” and rarely land or perch, it seems that their dependence on waterbodies for drinking still calls for frequent mechanical energy dissipation.

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Competing interests

No competing interests declared.

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Data availability

Raw and smoothed tracking data is available at <https://doi.org/10.6084/m9.figshare.20931934.v1>

Matlab analysis code is available upon request.

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