Contribution of slow motion video for an in flight behavioral study in the Common Swift *(Apus apus)* during the breeding period

Part 2 Foraging

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Abstract

In 2017, 2018 and 2019, 111 mornings were devoted to video recording in slow-motion the behavior of Common Swifts (*Apus apus*) flying over a small urban colony in the suburbs of Paris (breeding-station). After a dataset of in-flight grooming behaviors in Part 1, Part 2 presents data on aerial prey captures. Based on the very fast opening and closing of the beak on the prey, 1200 captures could be identified out of 721 videos.

The foraging flight, filmed between 10 and 30 m from the ground, has a sinuous path where short flapping flights with an average duration of 1 s alternate with short gliding flights with an average duration of 1.4 s.

In fine weather, hot and windless, the Common Swift is foraging by spending on average more time gliding than flapping. But the two types of flight ratios

can vary greatly depending on the weather conditions.

We arbitrarily defined:
- just before prey capture, 3 types of flight (gliding, "horizontal" flapping, ascending flapping);
- at the very moment of prey capture, 2 head positions ("retracted" and "projected");
- just after prey capture, 3 types of flight (flapping, gliding, gliding with turn.

These 8 possibilities provide 18 combinations which are all represented in varying ratios, the most common being: ascending flapping - capture with head "projected" - gliding with turn.
The features of ascending flapping flight have been studied: initiation, path, average duration, wingbeat frequency...
Prey capture itself was detailed: head postures, body postures, captures in inverted flight, average duration of beak opening (0.0214 s) and closing (0.0113 s)...

The 120 captures (10% of the total) where prey is visible allowed two calculations: the average speed of the bird at the capture time (7.9 m/s) and the average prey-to-bird distance (17 cm) when the bird begins to open its beak.
Five videos show that, in individuals at least 1 year old, prey selection can be done not only before capture by a last-minute renunciation but also after capture by an instant rejection of the prey.
After capture, the bird retains or adopts a gliding flight often marked by a turn keeping it in a foraging area potentially suitable for capture.

Videos with close sequences of prey captures were used to calculate the average length of the intervals between two successive catches (3.00 s).

From mid-June to the end of July, 34 videos show prey captures made by adults feeding chicks. The transport in the mouth cavity of the food ball (bolus) does not seem to have a significant impact on the prey capture abilities of swifts.

Data gathered in the spring of 2019 on a pre-nuptial migratory station (migration-station) of common swifts in Bretagne were compared with data from the urban breeding-station.

This comparison highlighted the impact of the study site, the size of prey available and local weather conditions on the qualitative and quantitative features of the prey captures.

Finally, as for grooming, a comparison could be made between Common Swift and Alpine Swift (*Tachymarptis melba*).

Despite a small sample size of 28 captures and a different context, it was possible to establish many similarities in the way the two species are foraging, as was already the case for in-flight grooming. Quantitative differences were regularly correlated with the difference between the two birds' average dimensions.

Introduction

In Part 1 conclusion on grooming, I had written: "A future paper will deal with the analysis of prey catches in flight as well as new data on some types of flights such as dihedral flight, inverted flight, duo-flight..." (Cornuet, 2019).

After the detailed description of various grooming behaviors, I thought that the study of captures would only be a few pages long. That's why I had considered adding the study of the various flight behaviors other than foraging flights.

In spring 2019, after the first part publication, I kept on shooting. At the end of April and beginning of May, I had the opportunity to film swifts in Bretagne during a migratory stopover. With the 234 captures filmed in this migration station, the idea of a comparison between the 2 stations seemed relevant to me.

In May, June and July, I resumed shooting in the breeding station. With the experience gained during the previous two years, I tried to increase the length of the videos by trying to film the same individual for longer. At the end of July, after the migration, I realized that I had more than doubled the number of capture clips (**Table 2**) with a nice sample of multiple captures.

At the end of August, as in 2018, I took some additional shots of the Alpine Swift (*Tachymarptis melba*) in the mountains. As for the grooming in flight, with 28 captures it became possible to compare the hunting of these two close species.

This is why Part 2 will be limited to the analysis of the 1200 captures from the breeding station, compared to the 234 data from the migration station and the 28 from the Alpine Swift hunt.

Studying an animal's diet involves answering two main questions:

- what does it eat?
- how does it get its food?

The Common Swift spends most of its life in the air. After leaving the nest, it will fly without ever landing until its first breeding attempts at about 3 or 4 years. From this age it will only land to breed (in May, June, and July in our latitudes) and will spend the remain of the year in the air (Hedenström, 2016).

How in these ways can we know the diet and eating habits of the Common Swift? D. Lack was one of the first to study its eating habits in the mid-fifties (Lack, 1956). To do so, he used the analysis of food balls or boluses brought to the nest by adults to feed their chicks.

He states that the Common Swift feeds exclusively in the air by hunting only Arthropods flying or carried away by air currents (aerial plankton).

Since this work, many authors have published results of bolus analysis in different locations of the breeding range.
Sometimes analysis of the feces of breeding adults complements bolus analysis (Gory, 2008).

Today we know that the Common Swift feeds mainly on insects and spiders to a lesser extent. Prey is excessively varied since at least 500 species of insects have been identified (Glutz von Blotzheim, 1980). These prey items are on average small in size (between 2 and 10 mm, rarely more).

Prey caught can vary enormously depending on:

- where they are captured (over water, over forest, over garrigue...) (Gory, 2008);
- weather conditions;
- individual preferences...

Since the beginning of this research, it has been accepted that prey identified in the boluses brought to the chicks also formed the basis of the adults' diet.
This choice is easy to understand: due to their small size, the observation distance and the speed of swifts foraging, it is impossible, except in exceptional situations, to directly identify the prey captured in flight.

This work is continuing to refine the qualitative and quantitative composition of the Common Swift's diet and to discover, for example, the likely impacts of reduced biodiversity and declining insect populations in relation to climate change, the massive use of pesticides and pollution in cities where swifts nest.

On the other hand, the aerial feeding behavior of the Common Swift is still poorly known. It is a bird whose diet cannot be studied in captivity, except for chicks. After flight, all prey are captured in the air until the end of its life.

The first way to study swift foraging is by observation with naked eyes or with binoculars. The paths of the foraging flight, rapid upward or sideways swings can be followed… (Lack, 1956)
Some captures are suspected, but their progress is so rapid that it escapes precise description.

Advances in digital cameras have made it possible to obtain capture images but never sequences of several images of the same capture. The reason is simple: since the act of capture is measured in hundredths of seconds, it is impossible to divide it into images with the frequency of 10 to 20 fps of the most sophisticated digital cameras.

In 2015, E. de Margerie and colleagues are developing a rotational stereo-videography monitoring device (De Margerie, 2015). In 2016 and 2017, in Rennes, C. Pichot (Pichot, 2017), led by E. de Margerie, uses this device to record the paths of common swifts foraging over a colony in the city of Rennes in Bretagne (France).

In her paper, C. Pichot describes the device (Pichot, 2017).

> This device involves a camera (Panasonic Lumix DMC-GH4, with a 200 mm focal length lens) in video mode, mounted on a tripod. The filmed image is divided in two by a system of mirrors, which gives a stereoscopic view of the filmed object and makes it possible to calculate its distance to the device. A head (Theodolite type) continuously records (frequency 50 Hz) the angles of azimuth and inclination of the camera in relation to the ground, using an electronic card (Arduino + DataLoggingShield). Exposure settings of the device are usually an aperture of f/11 to have a large depth of field, an exposure time of 1/1000 s to 1/1300 s to freeze animal movement, and a sensitivity of 800 to 1600 iso. The video format is 2K 30p 50M (1920 x 1080 px; 29.97 fps; 50 Mbps = 6 Megabytes/s). Focus is set at 150m (500ft) and is locked during recording.

From a qualitative point of view, video recordings allow them to establish a first behavioral dataset including:

- 6 types of flight: flapping, gliding...;
- 8 head positions: retracted, up, on the back…

These head positions are often assumed

to correspond to catching or grooming, but cannot be accurately described.

From a quantitative point of view, the device allows:

- to graphically draw the 3D path of the swift;
- to calculate continuously physical parameters (speed and acceleration) for each type of flight.

Following this research, two articles are published on the Common Swift's foraging flight.

A first paper (De Margerie, 2018) describes the 3D paths of the foraging flight and clarifies the notion of the VCS (Volume-Concentrated Search) strategy in aerial insectivores.

A second paper (Hedrich, 2018) explains, among other things, the ability of swifts to save their energy by making optimal use of air currents, such as thermal updrafts, so that gliding is used more often than flapping.

Drawing the 3D path and being able to know at any moment the speed and acceleration of a bird directly in the wild is a very big step forward in the knowledge of bird flight. It is an essential complement to laboratory measurements in flight tunnels on dead or captive specimens.

But with small birds such as the Common Swift, this method, for the moment, does not allow a detailed description of the aerial capture behavior of the Common Swift for two main reasons.

The first reason is that size and definition of the bird's details in the videos are poor: at a distance of 100 - 150 m, even with a resulting focal length of 200 mm (equivalent to a focal length of about 400 mm in FHD with the GH4's 4/3 sensor), the bird is too small to identify all the captures.

The second reason is that the frame rate of the video (29.97 fps) is clearly not enough to analyze capture behavior measured in hundredths of second.

This is why my close-up shooting technique at 180 fps allowing the description of behaviors and the recording of some parameters seems to me complementary to the rotational stereo-videography monitoring device.

Common Swift getting ready to catch a prey item

Methodology

Shooting periods and location

Observations and filming were made in Bois-Colombes (Hauts-de-Seine, France) from the roof of my pavilion by opening a Velux in the attic at a height of about 10 meters above the ground. Filming sessions occurred over 111 days in 2017, 2018 and 2019 (**Tables 1 and 2**), between 6:00 am and 11:00 am (four hours on average).

Four to five pairs of Common Swifts nest under the roofs of some of the surrounding pavilions and city buildings. The first individuals are regularly observed in the last week of April or the first week of May. These are breeding adults that settle quickly and discreetly in their usual nesting sites.

Numbers of birds increase from the last 10 days of May with the gradual arrival of 1st, 2nd and 3rd year immatures. As non-breeding birds with few exceptions, they mingle with breeding adults and prospect for potential nesting sites for the next few years. The colony's numbers drop sharply between 15 and 25 July due to migration.

Shooting gear

I used the Panasonic Lumix GH5 with the Nikkor 4/300 AFS lens by means of a Novoflex adapter. With a coefficient of 2, the equivalent focal length in 35 mm is 600 mm. Some shots were also taken with the TC14 (x 1.4) associated with the 4/300; the equivalent focal length in 35 mm is then 840 mm.

The GH5 settings are as follows:

- Mode d'exposition: M
- Rec Format: MOV
- Rec Quality: FHD 8bits 100M 30p

Table 1.
Calendar of the 111 days of shooting (in green) in 2017, 2018 and 2019

2017

May		June		July	
1	M	**1**	**T**	1	S
2	T	2	F	2	S
3	W	**3**	**S**	**3**	**M**
4	T	**4**	**S**	**4**	**T**
5	F	5	M	**5**	**W**
6	S	6	T	6	T
7	S	7	W	**7**	**F**
8	M	8	T	**8**	**S**
9	**T**	9	F	**9**	**S**
10	**W**	**10**	**S**	10	M
11	T	**11**	**S**	11	T
12	F	**12**	**M**	12	W
13	S	**13**	**T**	13	T
14	S	**14**	**W**	**14**	**F**
15	M	**15**	**T**	**15**	**S**
16	T	**16**	**F**	**16**	**S**
17	W	**17**	**S**	17	M
18	T	**18**	**S**	18	T
19	F	19	M	19	W
20	S	**20**	**T**	20	T
21	S	**21**	**W**	21	F
22	M	**22**	**T**	22	S
23	T	23	F	23	S
24	W	24	S	24	M
25	**T**	**25**	**S**	25	T
26	**F**	26	M	26	W
27	**S**	27	T	27	T
28	S	**28**	**W**	28	F
29	**M**	**29**	**T**	29	S
30	T	30	F	30	S
31	W			31	M

2018

May		June		July	
1	T	1	F	**1**	**S**
2	W	2	S	**2**	**M**
3	T	**3**	**S**	**3**	**T**
4	F	4	M	**4**	**W**
5	S	5	T	5	T
6	S	6	W	**6**	**F**
7	M	7	T	**7**	**S**
8	T	**8**	**F**	**8**	**S**
9	W	9	S	**9**	**M**
10	T	**10**	**S**	10	T
11	F	11	M	11	W
12	S	12	T	**12**	**T**
13	S	**13**	**W**	**13**	**F**
14	M	**14**	**T**	**14**	**S**
15	T	**15**	**F**	15	S
16	W	**16**	**S**	16	M
17	T	17	S	17	T
18	F	18	M	**18**	**W**
19	S	19	T	**19**	**T**
20	S	**20**	**W**	20	F
21	M	21	T	21	S
22	T	**22**	**F**	22	S
23	W	**23**	**S**	23	M
24	T	**24**	**S**	24	T
25	F	**25**	**M**	25	W
26	**S**	**26**	**T**	26	T
27	S	**27**	**W**	27	F
28	M	**28**	**T**	28	S
29	T	**29**	**F**	29	S
30	**W**	**30**	**S**	30	M
31	**T**			31	T

2019

May		June		July	
1	W	**1**	**S**	1	M
2	T	**2**	**S**	**2**	**T**
3	F	3	M	**3**	**W**
4	S	4	T	**4**	**T**
5	S	5	W	**5**	**F**
6	M	6	T	**6**	**S**
7	T	7	F	**7**	**S**
8	W	8	S	8	M
9	T	**9**	**S**	**9**	**T**
10	F	**10**	**M**	**10**	**W**
11	S	**11**	**T**	11	T
12	**S**	12	W	12	F
13	**M**	13	T	13	S
14	**T**	**14**	**F**	**14**	**S**
15	**W**	**15**	**S**	**15**	**M**
16	**T**	**16**	**S**	**16**	**T**
17	F	**17**	**M**	**17**	**W**
18	S	18	T	18	T
19	S	19	W	19	F
20	M	20	T	20	S
21	**T**	**21**	**F**	**21**	**S**
22	**W**	**22**	**S**	**22**	**M**
23	**T**	**23**	**S**	**23**	**T**
24	F	24	M	**24**	**W**
25	**S**	**25**	**T**	**25**	**T**
26	**S**	**26**	**W**	26	F
27	M	**27**	**T**	27	S
28	T	**28**	**F**	28	S
29	W	**29**	**S**	29	M
30	T	**30**	**S**	30	T
31	**F**			31	W

Table 2.
Distribution of capture videos in 2017, 2018 and 2019

	2017	2018	2019	TOTAL
Number of matinee shootings	33	32	46	111
Total number of clips processed and analyzed	540	845	1038	2433
Clips number showing one or more captures	177	169	375	721
Number of captures analysed	255	215	730	1200

- Variable Frame Rate: 180 fps
- In-Body Image Stabilizer: focal lens 300mm
- ISO sensitivity: 400
- Photo Style CNED:
  - Contrast: - 5
  - Sharpness: - 5
  - Noise Reduction: 0
  - Saturation: - 5
  - Hue: 0
- Lens is usually closed at f8
- Shutter speed from 1/400th to 1/2000th
- On clear sky, I overexpose to make the bird not just a black silhouette on a white sky.

Hybrid cameras have an electronic viewfinder. Manual focus is made easier by Focus Peaking, a function that displays a brightly colored border in the viewfinder on the contours of objects in the sharpness plane.

For manual focusing on blue sky, I chose a monochrome display with a golden yellow Focus Peaking. Thus I know that the bird will be in focus when, on the light grey background of the monochrome sky, the dark body of the flying Swift is delimited by a golden yellow border.

Is the variable rate of 180 fps enough for properly filming a Swift in flight ?

The maximum cadence on the GH5 is 180 fps. The video played at 30 fps shows a 6 times slow motion which is suitable for most birds in flight. However, this is hardly enough for swift because the bird is not very large (42 to 48 cm in wingspan), its flight is fast with sudden changes of direction and sharp accelerations. I get a better reading comfort and consequently a more accurate analysis of the videos by applying a software slowdown of 50%. In the editing software, slow motion is produced by creating intermediate images by interpolation. For the swift, the best compromise would be to film at a variable rate of 360 fps. Specialized cameras (Photron, Phantom,...) are suitable for such performance and even well beyond. Apart from their costs that are disproportionate to those of a GH5, they would not be suitable for tracking a swift in flight because of their ergonomics: without an electronic viewfinder, they do not allow, for example, the tracking (framing and focusing) of a swift in flight.

What additional information does the 180 fps slow motion bring to the photography?

Let's take the example of the 3 photographs on pages 139, 143 and 146. We see a swift in flight with its beak open, preparing to capture an insect flying a few centimetres in front of it.
However, this type of image can lead misinterpreting the hunting mode of swift. Indeed, I was very surprised to read on pages of reputable ornithological Websites that swifts were hunting with their beaks open! This is a false and surprising statement in 2018, knowing the problem had been solved since for decades by eminent ornithologists (Lack, 1956; Géroudet, 1980; Mayaud 1936…). From the hundreds of shots I succeeded in filming in slow motion, it is clear that the time taken by the bird to open and close the beak is so short that it is measured as hundredths of second. The slow motion video therefore provides formal proof that swift keeps its beak closed between two catches while hunting.

Shooting technique

The Common Swift moves quickly through the sky, on average at 10 m/s in spring on its breeding site. It cannot be tracked with the camera attached to a tripod with a fluid head. Instead, working with freehand as in photo, standing and stable on your legs is necessary to be reactive and effective in the follow-up movements of the bird.

I practiced photographing the Common Swift in flight between 2007 and 2012 using always the same 4/300 AFS with an autofocus Nikon D2X and then a Nikon D3. When the autofocus system catches the bird, a burst at 5 or 10 fps usually produces sharp images.

From 180 fps video devices, no current autofocus system is able to continuously adjust the focus on a subject that moves as fast as swift. Moreover, the autofocus is automatically disabled on GH5 when it is set to variable frame rate.

For good manual focusing, one needs a lens with a flexible and precise focusing ring. The most difficult situation to manage is when the bird arrives from the front towards the operator because it is necessary to both keep the bird in the frame and as the same time adjust the focus continuously as the bird approaches.

Video processing

Video processing (colorimetry, sharpness) as well as image analysis and counting were done using the Apple's Final Cut Pro X™ editing software, displaying time in images. From Apple's Compressor™ software, an export into a sequence of TIFF images made the production of the thumbnails sheets describing the behaviors easier.

Common Swift getting ready
to catch a prey item

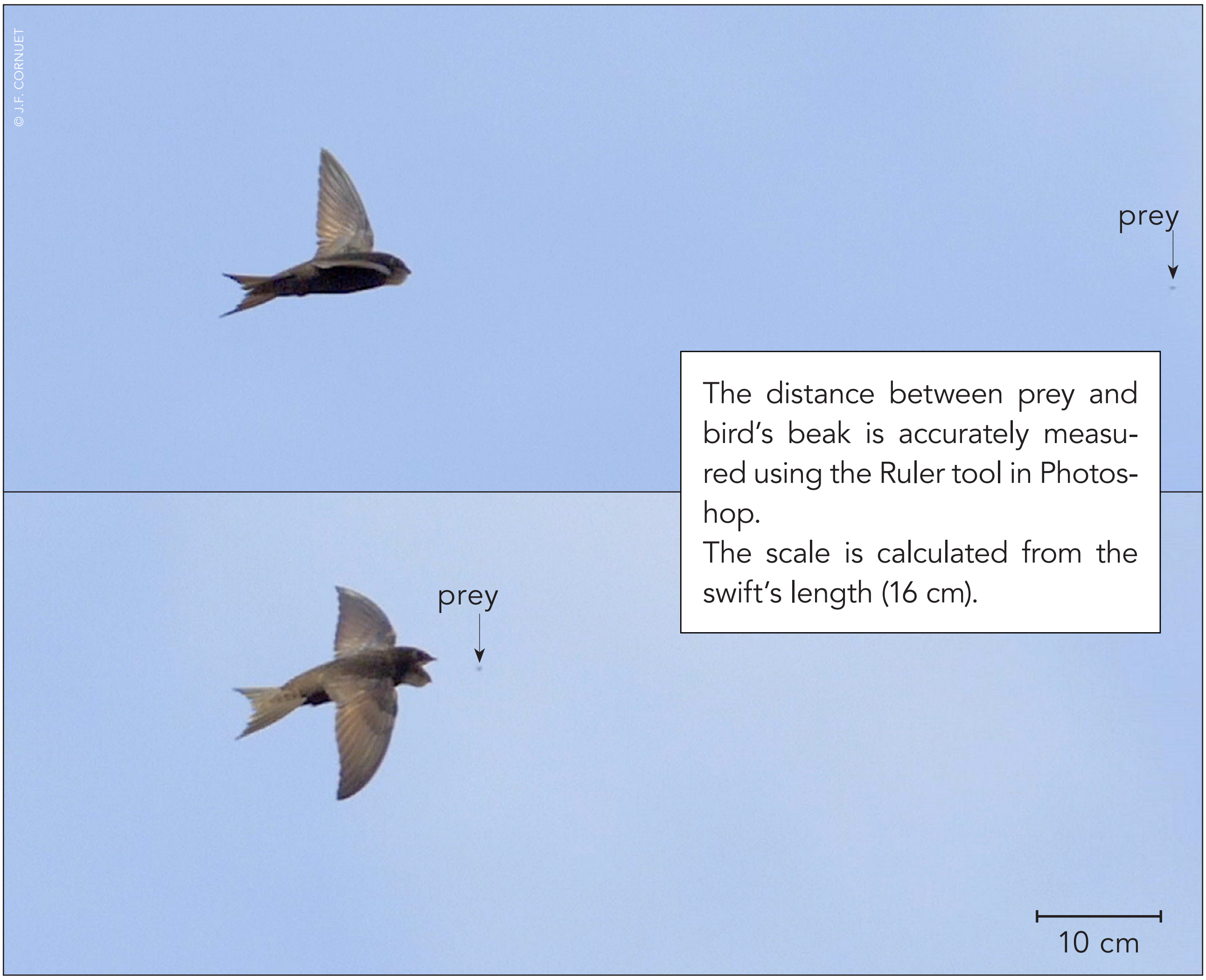
Video analysis

It was mainly done in the FCPX editing software where the markers were very useful for time calculations (opening-closing the beak, gliding-flapping...). On the original videos that were not slowed down in post-production, the duration of the behaviors and, for some flights, the wingbeat frequency were calculated, based on the frame duration (1/180 s): for example, a behavior that occurs over 240 images lasts 240/180 = 1.33 s.

Adobe Photoshop™'s Ruler tool was used to measure distances on video screenshots where prey was visible in the time before capture.

In this way it was possible to calculate:

- the average speed at which swift travelled the last decimeters separating it from its prey;
- the prey-to-bird distance when swift begins to open its beak.



The distance between prey and bird's beak is accurately measured using the Ruler tool in Photoshop.
The scale is calculated from the swift's length (16 cm).

Comparison between 2 stations

At the end of April - beginning of May 2019, I filmed common swifts in migratory stopover foraging over coastal wetlands in the Bay of Audierne (Tréogat, Finistère, France).
It looked like a good idea to compare the foraging strategies of these birds on the two stations:

- migration-station in Bretagne;
- breeding-station in Île-de-France.

Comparison with the Alpine Swift

In August 2018 and 2019, near the summit of La Bourgeoise mountain (Samoëns, Haute-Savoie, France), at an altitude of 1760 m, I filmed groups of Alpine Swifts (*Tachymarptis melba*) hunting over grassy ridges. I was able to shoot 28 prey captures in slow motion with many similarities to those observed in Common Swift.

Common Swift

Alpine Swift

1. Foraging flight

Due to the small size of its prey, the Common Swift spends a large part of its daytime flying time foraging. This activity increases if it is an adult that has to feed chicks and at the same time must provide for its own food needs.
In the study site, being 10 m above the ground, I was able to shoot many foraging flights, i.e. with effective prey captures, in an aerial zone between 10 and 30 m of altitude.
Foraging flight near a colony has been described (De Margerie, 2018). It is a tortuous flight with a sinuous path where the bird follows a series of prey captures by describing circles with many turns.
On my videos, the prey captures were identified by the beak's opening and closing, often in combination with:

- changes in flying patterns;
- particular postures of the bird's body;
- head projections.

Among the 1200 captures identified and studied by the above criteria, the prey is visible on 120 (10%) of them. These are all successful. The Common Swift is therefore a very efficient hunter and the above criteria seem to be valid for the identification of all captures.
To characterize the foraging flight, I have selected 52 videos with 4 to 15 successive captures. It is thus well about swifts in full active hunting.

Common Swift in flapping flight

These 52 videos represent a cumulative real time of 16 min and 20 s with 332 identified captures.
During all its aerial moves, the Common Swift switches between two flights: the flapping and the gliding flight.

1.A. Flapping flight

Flapping flight is an active flight with lift and propulsion involving a complete cycle of wing beats, with both wings flapping synchronously (Pichot, 2017). The flapping amplitude and frequency are variable according to the bird's needs.
Of the 52 videos selected, 455 flapping flight bouts were identified. The average duration of a flapping flight bout is 1.0 s. Among these 455 bouts, only 14 (2.1%) are longer than 3 seconds with a maximum value of 10.2 seconds.

1.B. Gliding flight

Gliding is a passive flight without propulsion where both wings are stretched at body height in a more or less symmetrical way (Pichot, 2017). Depending on the angle that the wings form with the transverse plane, the wingspan is more or less important.
Of the 52 videos selected, 402 gliding flight bouts were identified. The average duration of a gliding bout is 1.4 seconds. Among these 402 bouts, only 34 (8.5%)

Common Swift in gliding flight

are longer than 3 seconds with a maximum value of 12.5 seconds.

1.C. The gliding and flapping distribution

Taking the 52 videos as a single sequence of 16 min and 20 s, the swifts on foraging spend:

- 53 % of the time in gliding flight;
- 47 % of the time in flapping flight.

This apparent relative balance between the two types of flight is misleading.
If we compare the percentages of the two types of flight in each of the 52 videos:

- 1/3 of the videos show a dominance (60-90 %) of gliding over flapping flight;
- 1/3 of the videos approach the gliding to flapping balance (40-60 %);
- 1/3 of the videos show a dominance (60-90 %) of the flapping over the gliding.

One of the possible explanations for these differences must be sought in the weather conditions of the day and time of the shooting: air temperature, wind strength, sunshine and cloud cover conditioning the abundance and intensity of air currents and more particularly thermal updrafts.

Let's take the morning of June 9, 2019 as an example. It was particularly well suited for shooting since 12 of the 52 videos were shot that day, with 81 captures in total.

On 11 of these 12 videos the flapping flight largely exceeds the gliding flight. However, on 9 June 2019, the sky is overcast all morning and temperatures will remain cool for the month of June (between 12°C at 06:00 and 17°C at 11:00).
These conditions are not really good for the development of thermal updrafts that favour gliding.

Review
The foraging flight with prey captures of the Common Swift in good weather, with no wind, over a small urban colony between 6:00 and 11:00 a.m. consists of short flapping flights (average duration of 1.0 s) switching with short gliding flights (average duration of 1.4 s).
From one foraging flight to another, the respective proportions of gliding and flapping bouts can vary very significantly depending on:

- the temperature;
- the air masses movements;
- the prey availability;
- the food needs of the moment (feeding chicks or not)...

Discussion
The flight muscles involved in the wing movements of flapping flight consume more energy than the muscles involved in maintaining the spread wings of gliding flight (Tobalske, 2007; Norberg, 1996).

If a bird wants to reduce its energy expenditure, it is therefore in its interest to favour gliding over flapping.

Using rotational stereo-videography monitoring device over a large breeding colony (Hedrich, 2018), it was found that swifts:

- spent only 25% of their time in flapping flight;
- spent the majority of their time (71%) in gliding, during which they were able to extract enough environmental energy (thermal updrafts...) to pay for the cost of flying while foraging.

2. Flights, paths and postures

When the Common Swift explores a foraging area, two main situations occur:

- situation 1: the path of the prey coincides with that of the swift;
- situation 2: the path of the prey differs from that of the swift.

In situation 1, the bird can maintain its flight path and flight type (gliding or flapping). Only the opening and closing of the beak indicate capture. These are the most discreet captures and therefore the most difficult to detect on a video. Fortunately in a certain number of situations, the bird also makes a projecting movement of the head towards the prey when the beak is opened/closed.

In situation 2, the bird changes its flight path and often its flight type to reach the prey.

Each capture is thus a sequence of actions where 3 times are distinguished: before the capture, the capture itself and after the capture.

2.A. Flights and paths just prior to capture

Just prior to capture, the bird may be either in gliding or flapping flight with a nearly "horizontal" path.

But in 44 % of captures, the bird suddenly changes its behavior: it rises with a ascending flapping flight to capture a prey item.

Before capture, three types of flight can be defined arbitrarily:

- gliding flight;
- "horizontal" flapping flight;
- ascending flapping flight.

2.B. Postures at the catching time

Two postures can be distinguished at the catching time:

- posture 1: the bird keeps its head in its usual position ("retracted" head);
- posture 2: the bird makes a head extension movement by projecting the head towards the prey, with the beak wide open ("projected" head).

This head projection can be forward, up, down or sideways. It may or may not be accompanied by a contortion of the bird's entire body.

At the capture time, two head postures are considered:

- "retracted" head;
- "projected" head.

2.C. Flights and paths just after capture

Just after capture, the bird can stay or switch to gliding or flapping flight.

But in more than a third of captures, the bird changes path by making a gliding turn with a special look.

After capture, three types of flight can therefore be arbitrarily defined:

- flapping flight;
- gliding flight;
- gliding flight with a turn.

Table 3 shows the 18 possible combinations with these 8 options, ranked according to the decreasing number of catches.

Table 3.
The 18 combinations of the 8 types of flight and postures before, during and after capture

Flight before capture - Head Flight after capture	Number of captures	Percentage
1. Ascending flapping flight - "Projected" head Gliding flight with a turn	279	23,25 %
2. "Horizontal" flapping flight - "Projected" head Flapping flight	220	18,33 %
3. Ascending flapping flight - "Projected head Flapping flight	181	15,08 %
4. "Horizontal" flapping flight - "Retracted" head Flapping flight	123	10,25 %
5. Gliding flight - "Projected" head Gliding flight	87	7,25 %
6. "Horizontal" flapping flight - "Projected" head Gliding flight	42	3,50 %
7. Gliding flight - "Retracted" head Gliding flight	40	3,33 %
8. Gliding flight - "Projected" head Gliding flight with a turn	35	2,92 %
9. Gliding flight - "Projected" head Flapping flight	32	2,66 %
10. "Horizontal" flapping flight - "Projected" head Gliding flight with a turn	32	2,66 %
11. Ascending flapping flight - "Projected" head Gliding flight	31	2,58 %
12. Ascending flapping flight - "Retracted" head Flapping flight	21	1,75 %
13. "Horizontal" flapping flight - "Retracted" head Gliding flight with a turn	16	1,33 %
14. "Horizontal" flapping flight- "Retracted" head Gliding flight	16	1,33 %
15. Gliding flight - "Retracted" head Gliding flight with a turn	15	1,25 %
16. Gliding flight - "Retracted" head Flapping flight	15	1,25 %
17. Ascending flapping flight - "Retracted" head Gliding flight with a turn	11	0,92 %
18. Ascending flapping flight - "Retracted" head Gliding flight	4	0,33 %
Total captures	**1200**	**100 %**

Just before capture:

- 81 % of the birds are in flapping flight, 54 % of which are in ascending flapping flight;
- 19 % are in gliding flight.

At the capture time:

- 78 % of the captures are made with a head projection;
- 22 % of captures are made without head projection.

Just after capture

- 50 % of the birds are in gliding flight, 64 % of which are in gliding flight with turns;
- 50 % are in flapping flight.

3. Flights, paths and postures just prior to capture

3.A. Capture after an ascending flapping flight

In 527 captures (43.9 %) the bird catches its prey after a particular flight: the ascending flapping flight. The aim of this flight is to reach a prey whose path is above that of the swift.

3.A.1. Ascending flapping flight triggering

If the bird is in gliding flight, the start of the ascending flapping flight is easily identified by the wings being set in motion.
If the bird is in flapping flight, the start of the ascending flapping flight is marked by more discrete features: ascending path, special flapping of the wings with different amplitude and frequency... The spreading of the tail rectrices is usually visible from the beginning of the ascent.
The ascending flapping flight is also marked by the visible tension of the bird, which does not seems to look away from the prey.

3.A.2. Path of the ascending flapping flight

The path is ascending with an altitude gain of a few meters. The capture marks the top of this path, which can decrease more or less depending on the efforts made by the bird and the type of flight that follows the capture (gliding or flapping). In a number of cases, therefore, a bell-shaped trajectory is possible (**Figure 1**).

3.A.3. Average duration of the ascending flapping flight

Out of the 527 captures preceded by an ascending flapping flight, a sample of 175 ascending flights was selected with a minimum number of 5 complete wing beating cycles as the main criterion.

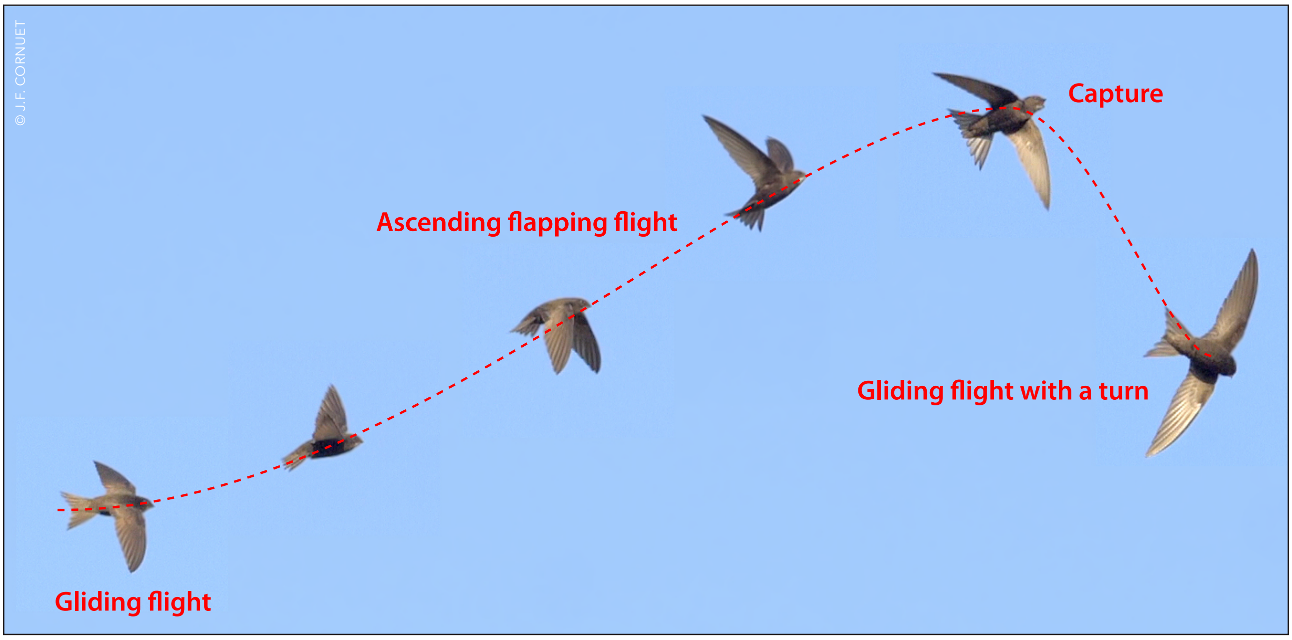


Figure 1.
Ascending flapping flight — "Projected" head — Gliding flight with a turn

Vidéo

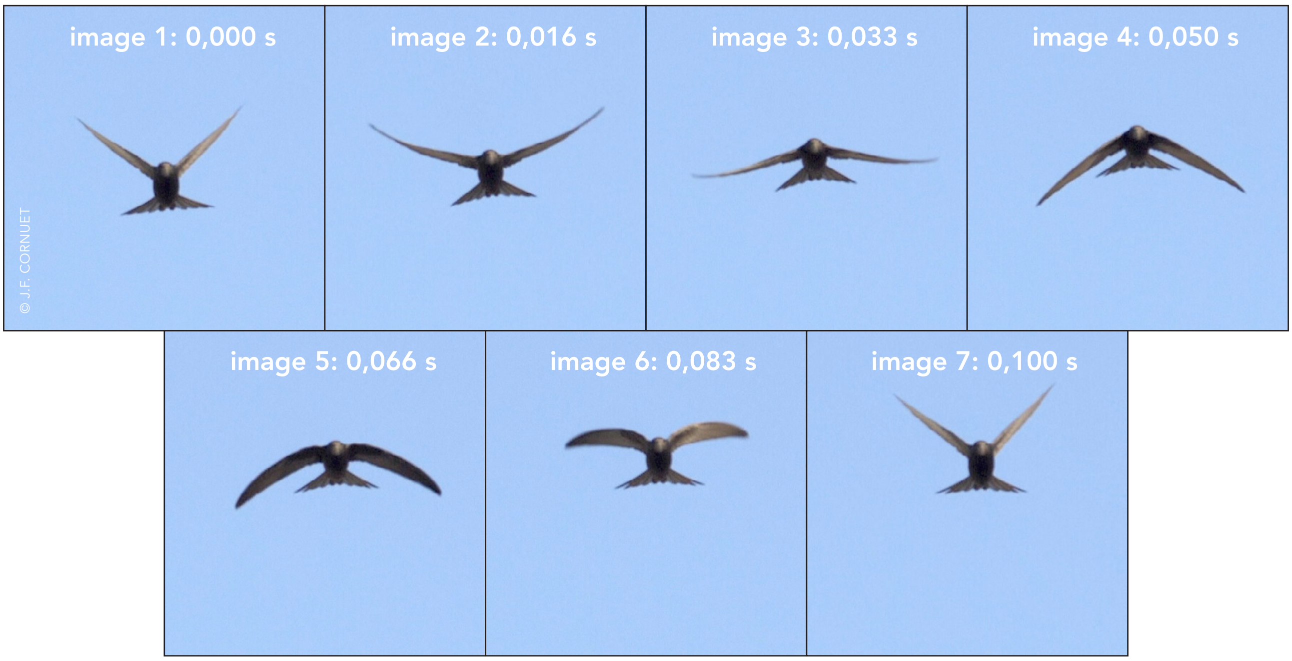


Figure 2.
Ascending flapping flight, frontview: a complete cycle is carried out in 0.100 s (frequency = 10 Hz)
Vidéo

With this sample of 175 ascending flapping flights:

- the minimum duration is 0.388 seconds;
- the average duration is 0.780 seconds;
- the maximum duration is 1.513 seconds.

3.A.4. Wingbeat frequency of the ascending flapping flight

The wings are beaten to rapidly raise the bird to reach the prey (**Figure 2**).
On the sample of 175 ascending flapping flights:

- the minimum wingbeat frequency is 6.0 Hz (6 complete cycles in 0.994 s);
- the average wingbeat frequency is 9.4 Hz;
- the maximum wingbeat frequency is 13.2 Hz (14 cycles in 1.061 s).

Depending on the circumstances, the beat amplitude is more or less strong. The tail is always well extended. However, the spreading of the tail rectrices usually serves to increase the lift and rather marks a slowing down and stabilization. We can therefore admit that during the ascending flapping flight, Swift seeks a compromise between the speed and precision of its path in order to cross the prey's path at the right time and in the right place.

If we compare the average frequency of the ascending flapping flight (9.4 Hz) with the average frequency (7.8 Hz) of the exploratory flapping flight (n = 100), it is about 20% higher.

3.A.5. Prey detection

The beginning of the ascending flapping flight can be considered as the moment when swift detects the prey. Since the duration is known, in order to calculate the distance travelled during this ascending flapping flight, it should be possible to measure the swift speed.
This distance would be the prey detection distance. Depending on the size of the prey it would then be possible to discuss the vision skills of the Common Swift.

3.A.6. Comparison of ascending flights in grooming and catching

On page 65 of Part 1 of the grooming article (Cornuet, 2019), a bell flight has already been described. Let's compare the two behaviors (**Figure 3**).

Both paths have an asymmetrical bell shape with an ascending and a descending part, but the two flights are differing by:

- the aim and the triggering of the flight;
- the asymmetry of the paths;
- the flight type.

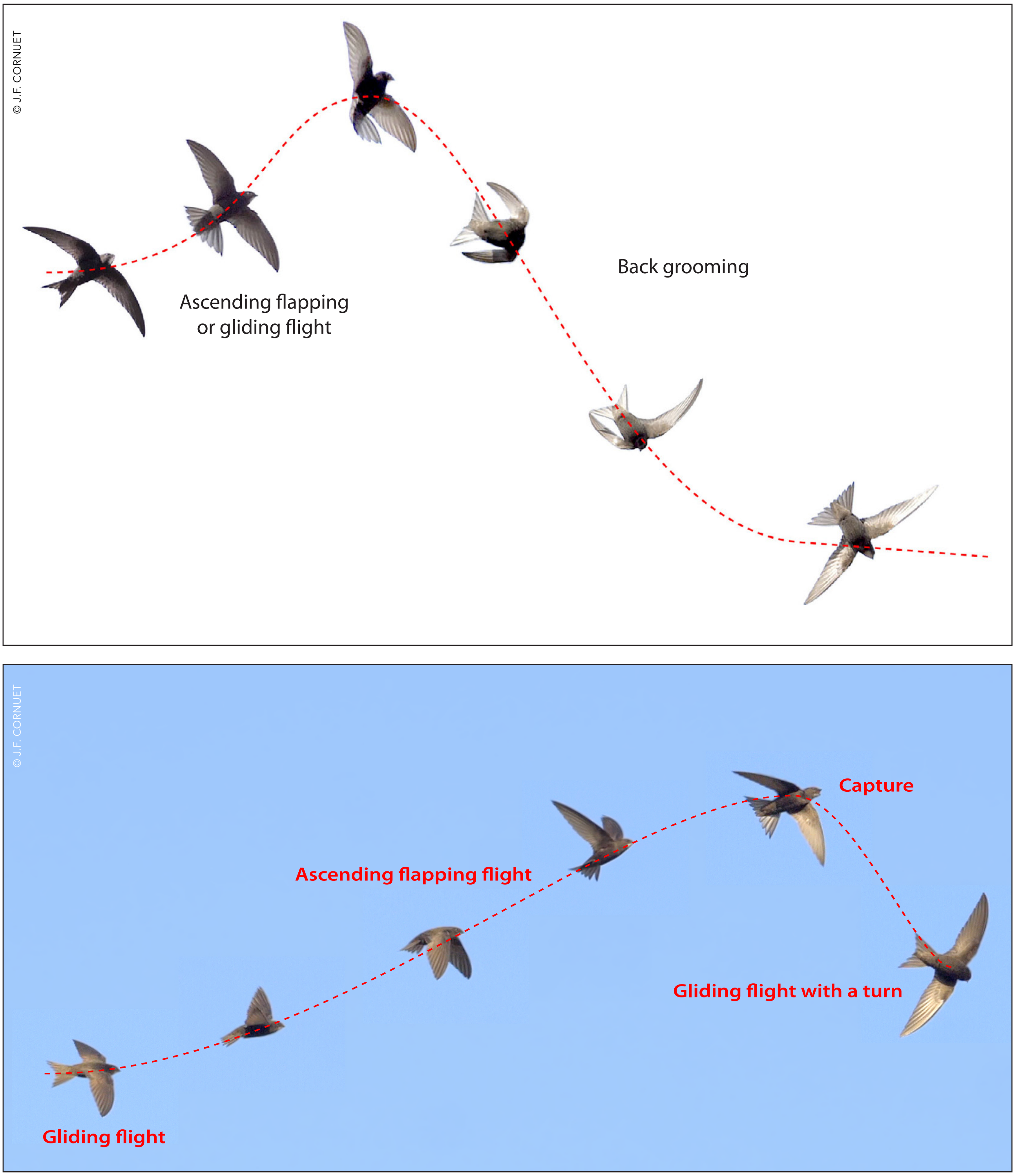


Figure 3.
Comparison between ascending flights in grooming (top) and in captures (bottom)

3.A.6.1. Aim and triggering of the behavior

Grooming: we have seen that in-flight grooming is always followed by a more or less important loss of altitude. The ascending part then appears as a forecast compensation intended to partially limit the loss of altitude.

The behavior is activated as follows:

- either internal and corresponding to a hygienic requirement to maintain the plumage in good condition;
- either external (parasites...).

In social contexts, it may be initiated by contagion/imitation of other individuals grooming (Garino, 1998).

Catching: Ascending flapping flight is for capturing prey. Its triggering is both internal (hunger or need to feed chicks) and external (visual detection of the prey).

3.A.6.2. Path asymmetry

Grooming: the ascending phase with an average duration of 0.89 s (n = 59) is followed by a longer descending phase whose duration depends on the type of grooming (see Part 1) with a clearly visible loss of altitude.

Catching: the ascending phase with an average duration of 0.78 s (n = 175) is followed by a very short descending phase depending on the type of flight adopted after capture (gliding or flapping) with little to no loss of altitude.

3.A.6.3. Flight type

Grooming: the ascending phase can be done as much in gliding as in flapping flight with a frequency of 7.5 Hz (n = 28). In both cases, the bird may stop for a very short time at the very beginning of its grooming. Note that in order to rise in gliding, the bird probably has to use lift (thermal or other) or headwind.

Catching: the ascending flapping flight with a frequency of 9.4 Hz (n = 175) is intended to converge swift's path with that of the higher prey. Just prior to capture, the bird may be gliding for a short time and stop briefly in order to best position itself to catch the prey by opening the beak wide.

After capture, the flight can be flapping or gliding with or without a turn.

Conclusion: with better defined characteristics the ascending flapping flight for a capture appears to be a more stereotypical behavior than the ascending flight before a grooming. It is also a much more frequent behavior in the daytime activities of the swift.

3.A.7. Ascending and diving flight

Can the Common Swift dive to capture a flying prey below it?

In this study, no such captures were recorded:

- either this result is related to the swift's environment (lodges, buildings and gardens);
- or it is an exceptional behavior;
- or it is a behavior that is not observed in the Common Swift regardless of the foraging environment.

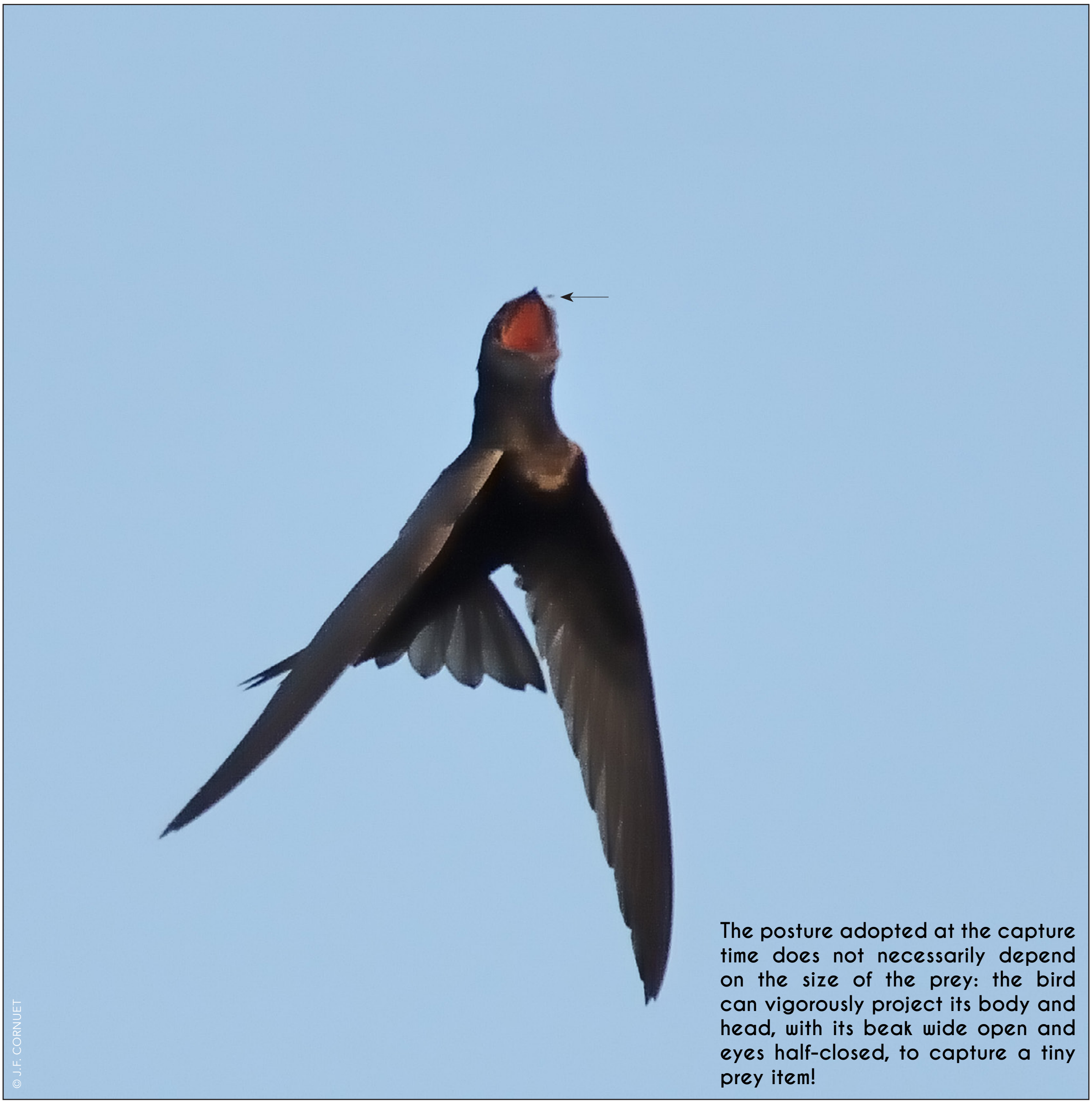
When swift hunts between 1 and 30 m in altitude, it may be easier for it to detect prey measuring a few millimetres above it because they are more visible on the sky background than prey located below it on a heterogeneous background (tile roofs, vegetation...).

Diving on its prey also results in a loss of altitude increased by the bird's speed, which it then has to compensate by rising

again in flapping flight.
During the foraging flight, the Common Swift switches between:

- gliding phases during which it can lose some altitude depending on the movement of air masses
- flapping phases during which it has the possibility to gain altitude in order to maintain itself in the foraging area.

Captures preceded by an ascending flapping flight thus offer the double advantage of linking a capture and a rapid gain (0.78 s) in altitude of a few meters.
However, the Common Swift is well able to make diving flights followed by an ascending glide that can be almost vertical when returning to the nest located under a roof overhang. But I doubt that this type of diving flight is regularly used for catching, or in other foraging conditions: for example beyond 30 m when the loss of altitude is no longer a real problem.
The catching posture with the swift standing up to catch its prey is certainly easier to achieve than a downward extension of the head and body (**Table 4**).
It can also be noted that in flight clashes between swifts, the «aggressor» always attacks the « victim « from underneath and not from above.



The posture adopted at the capture time does not necessarily depend on the size of the prey: the bird can vigorously project its body and head, with its beak wide open and eyes half-closed, to capture a tiny prey item!

3.B. Capture after an "horizontal" flapping flight

In 449 captures (37.4 % of the 1200) the bird catches its prey in a flapping flight that appears to be straight and more or less "horizontal".
Either the bird's path corresponds to that of the prey, or discreet wing and tail movements allow it to position itself on the prey's path.
In 155 captures (35 % of 449) only the opening/closing of the beak signals capture (**Figure 4**).
In 294 captures (65 % of the 449) beak opening/closing is done with a head projection.

3.C. Capture after a gliding flight

In 224 captures (18.7 % of the 1200) the bird catches its prey during a glide.
Either the bird's path corresponds to that of the prey, or discreet wing and tail movements allow it to position itself on the prey's path.
In 70 captures (31 % of 224) only the opening/closing of the beak signals capture (**Figure 5**).
In 154 captures (69 % of the 224) beak opening/closing is done with a head projection.

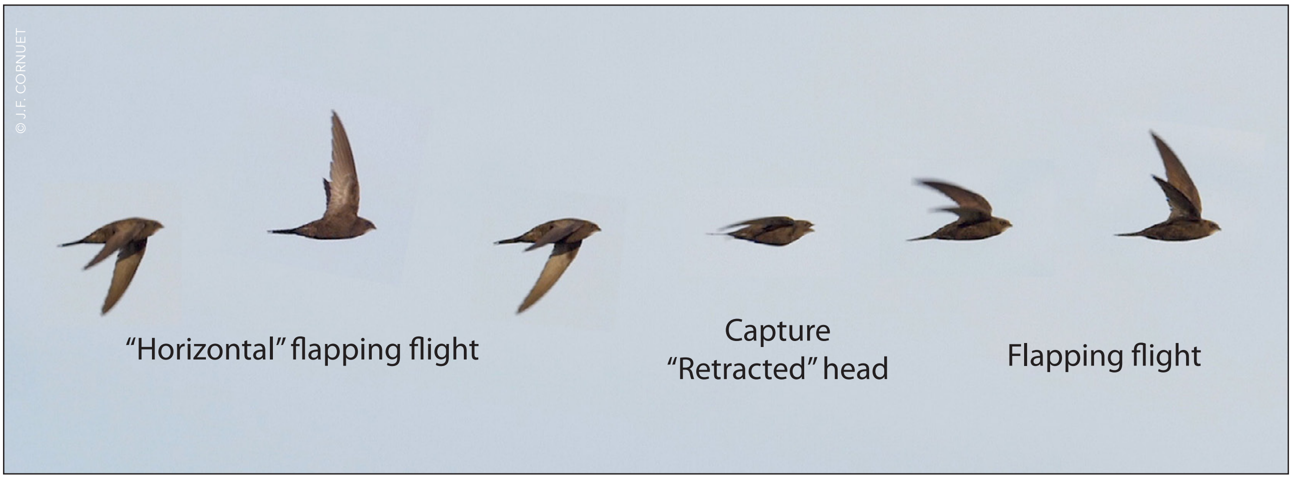


Figure 4.
"Horizontal" flapping flight - Capture with "Retracted" head - Flapping flight
Vidéo

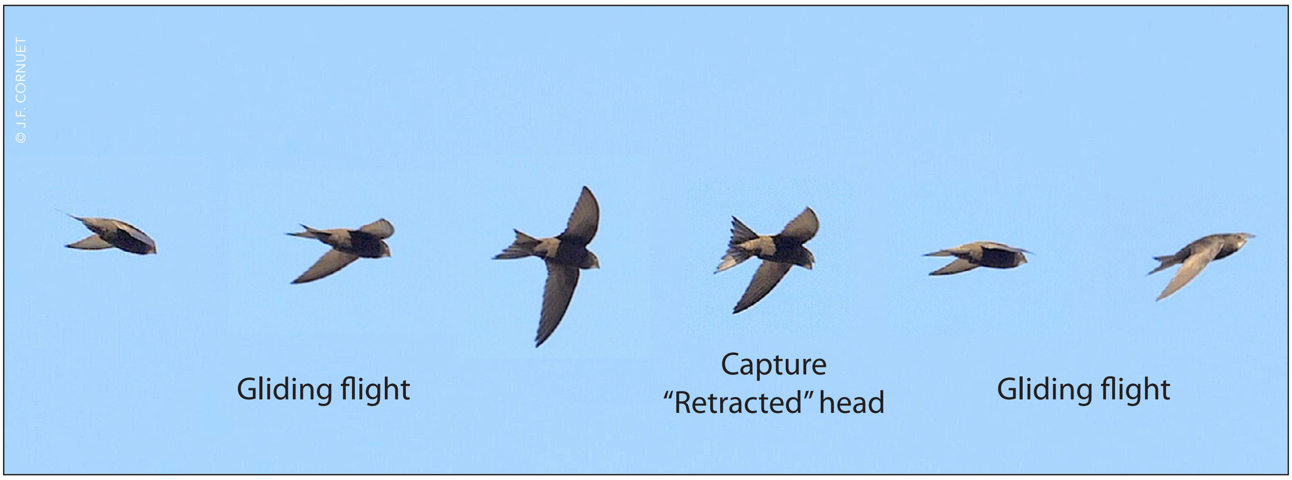


Figure 5.
Gliding flight - Capture with "Retracted" head - Gliding flight
Vidéo

4. Capture

4.A. Head postures

4.A.1. Head « projection »

Two head postures can be defined:

- the head "retracted" posture: this is the usual position of the head out of catches; it is retained in 271 catches (21.7 % of the 1200);
- the head "projected" posture: it is observed in 939 catches (78.3 % of the 1200).

The head can be "projected" in 4 directions: front, top, side and bottom (**Table 4 & Figure 6**).

This ability to neck extension had already been observed in the Common Swift in flight in some types of grooming (back grooming, rectrices preening...).

It's a common feature among birds. The Common Swift uses it here to increase the success rate of its captures.

It is not surprising that the "head forward projection" prevails since it is in the flight direction of the Common Swift.

The posture adopted at capture time is not necessarily related to the prey size: the bird can vigorously project body and head, with beak wide open and eyes half-closed, to capture a tiny prey item! (**Figure 6-UPWARD**).

Table 4.
Distribution of the 4 directions of the head's "projection"

	CAPTURES NUMBER	PERCENTAGES
Head forward projection	409	43,5 %
Head upward projection	278	29,6 %
Head sideward projection	245	26,1 %
Head downpward projection	7	0,8 %
TOTAL	939	100 %

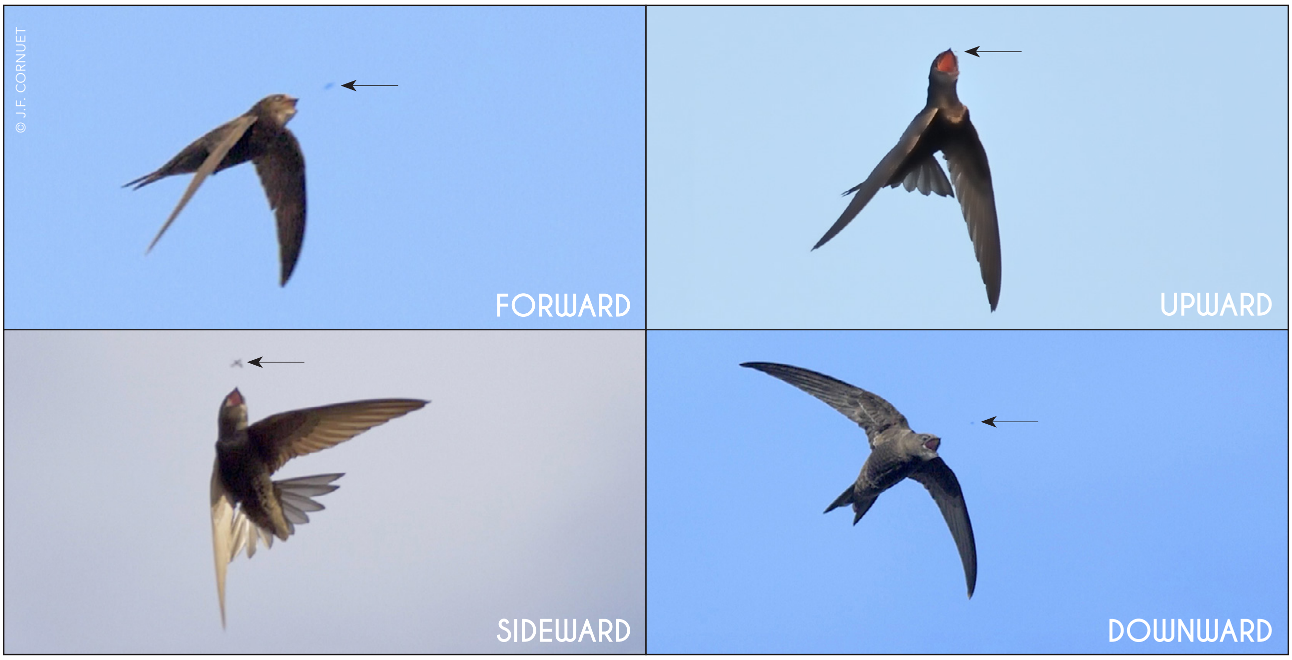


Figure 6.
The 4 types of head «projection» at the capture time (prey at the end of the arrow)

The very low head-down projection rate confirms what has been written about the scarcity of catches preceded by diving flight.

4.A.2. Beak and gap

The Common Swift has a small blackish triangular beak that can open wide under the eye to reveal a large, bright red gap.

The beak opening amplitude is variable and is not directly related to the size of the prey since a maximum amplitude can be observed for very small prey (**Figure 7 top**).

The prey sticks to the oral mucosa covered with sticky saliva and is then swallowed.

4.A.3. Eyelids

The Common Swift has eyelids to protect the eyes. At the capture time, when it opens its beak very wide, eyelids often close partially (**Figure 7 below**).
Heinroth observed that young swifts close their eyes while feeding and capture insects in the nest by groping with eyes closed. He suggested that swifts cannot adjust their eyes to « close-up vision» and that they close their eyes to avoid possible contact with the cornea (Heinroth, 1926).
However when the Common Swift skims the water with its beak wide open to drink, it certainly keeps its eyes wide open for safety.

Figure 7.
Maximum opening of the gap (top) and partial closure of the eyelids (bottom)

4.B. Body postures

4.B.1. Whole body projection

The head projection is often followed by an extensional movement of the whole body with the wings lowered and the rectrices widely spread out in a fan shape (**Figure 7**).

4.B.2. Captures in inverted flight

A bird is in inverted flight when its body rotates and it finds itself flying on its back in flapping or gliding flight (**Figure 8**). The inclination of the frontal surface becomes more than 90° to the horizon (Pichot, 2017). It returns to the initial position by a movement in the opposite direction without making a complete turn (Oehme, 1968).

Figure 8.
Inverted flight: 9 examples showing the diversity of wing and head positions

It is therefore limited to half a roll of 180° maximum.
Depending on the type of flight, two different procedures are used by the Common Swift to rotate:

- if the bird is in gliding flight, the half-turn can be done with the wings fixed and kept spread out;
- more frequently, if the bird is in flapping flight, the bird flips in reverse flight by rotating the wings (**Figure 9**) while keeping the head fixed or slightly tilted to the side.

The head is not upside down as Oehme drew it in 1968. But he could not see this detail in the images of his films because the swift shape was too small (Oehme, 1968).

In Common Swift, inverted flight is regularly observed in a social context. It seems to mark a mistrust of the individual who displays it in relation to an individual whose trajectory is close to its own. During screaming parties, individuals may find themselves momentarily in inverted flight, as well as during banging and snagging in flight.

Inverted flight is a common practice among some bird species.
Depending on the species and situation, inverted flight can be used to:

- quickly losing speed before landing (Palmipeds...);
- capturing prey (Bee-eaters, Raptors...);
- escaping from a predator (Pigeons...);
- courtship (Raven, Lapwing, Raptors...);
- exchanging prey between partners or between adults and youngs (Raptors...).

Figure 9.
Body rotation of the Common Swift during the passage in inverted flight. The head remains fixed.

Since the air is a 3D environment, it is natural that the inverted flight is part of the flight options used by the birds.

Of the 1200 captures, 46 (3.8 %) show a inverted flight:

- 22 captures take place in a inverted flight (**Figure 10**);
- 24 captures are followed immediately by an inverted flight (**Figure 11**).

Inverted flights are equally clockwise and counterclockwise. The 46 captures are made during a flapping flight and each inverted flight is produced by a wings rotation.

In the Common Swift, the inverted flight is therefore used not only to communicate in a social context but also to ensure the success of certain captures: better positioning, slowing down...

Figure 10.
Captures in inverted flight
Vidéo

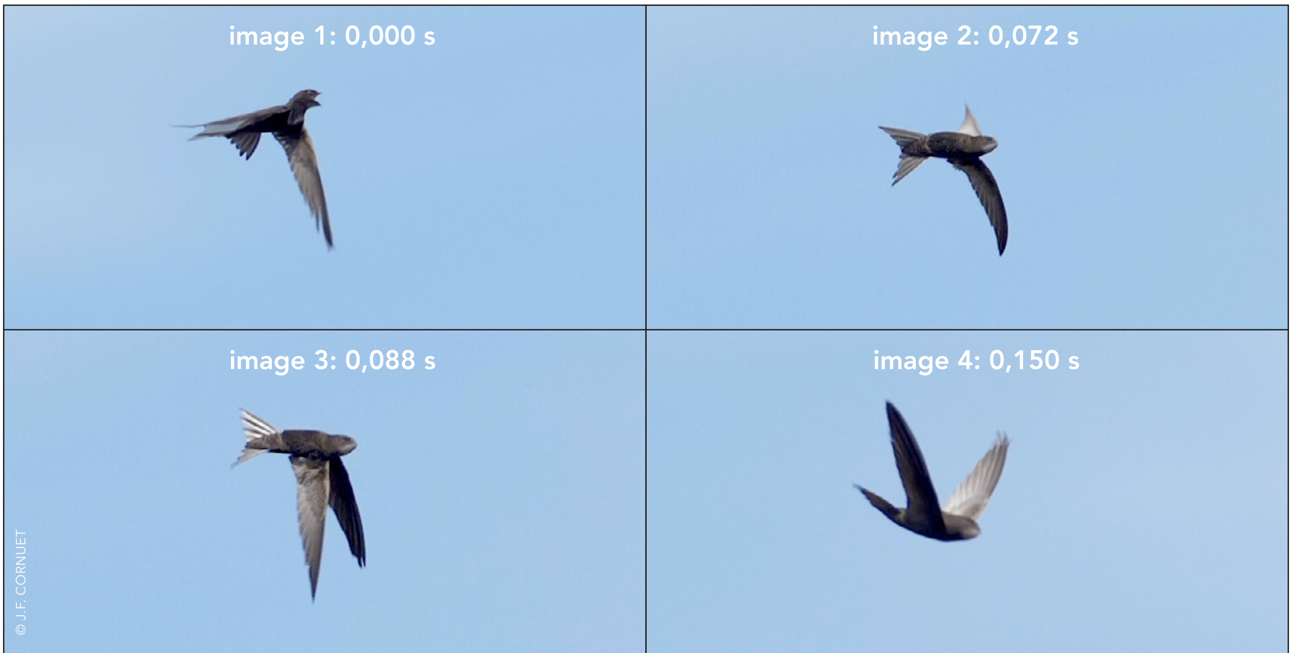


Figure 11.
Capture followed by inverted flight
Vidéo

4.C. Beak opening and closing

4.C.1. Foraging is done with closed beak

The 1200 videos clearly show that the Common Swift forages with its beak closed and opens it only for a very brief moment only at the capture time, even when the captures are made in very short sequences.

In flight the Common Swift opens its beak in at least six situations.

1. It half-opens its beak when it screams its shrill calls: thus in screaming parties, one or more individuals can be observed with their beak half-opened. This is air exhaled to produce the sounds (**Figure 12-1**) and the beak opening time is variable.
2. Above 30°C, swifts ensure their thermoregulation by taking the legs out of the ventral plumage. They may in some cases open the beak to try to evacuate excess internal heat (**Figure 12-2**) (Neumann, 2016)
3. Exceptionally, the Common Swift may shake its head with its beak wide open to reject prey that has just been captured or to clean its gap (**Figure 12-3**).
4. The Common Swift opens and closes its beak for each capture (**Figure 12-4**).
5. The Common Swift can half-open its beak in flight for various grooming (preening the rectrices...).
6. **To drink, the Common Swift takes water, with its beak wide open, by skimming the surface of a pond, lake or marsh.**

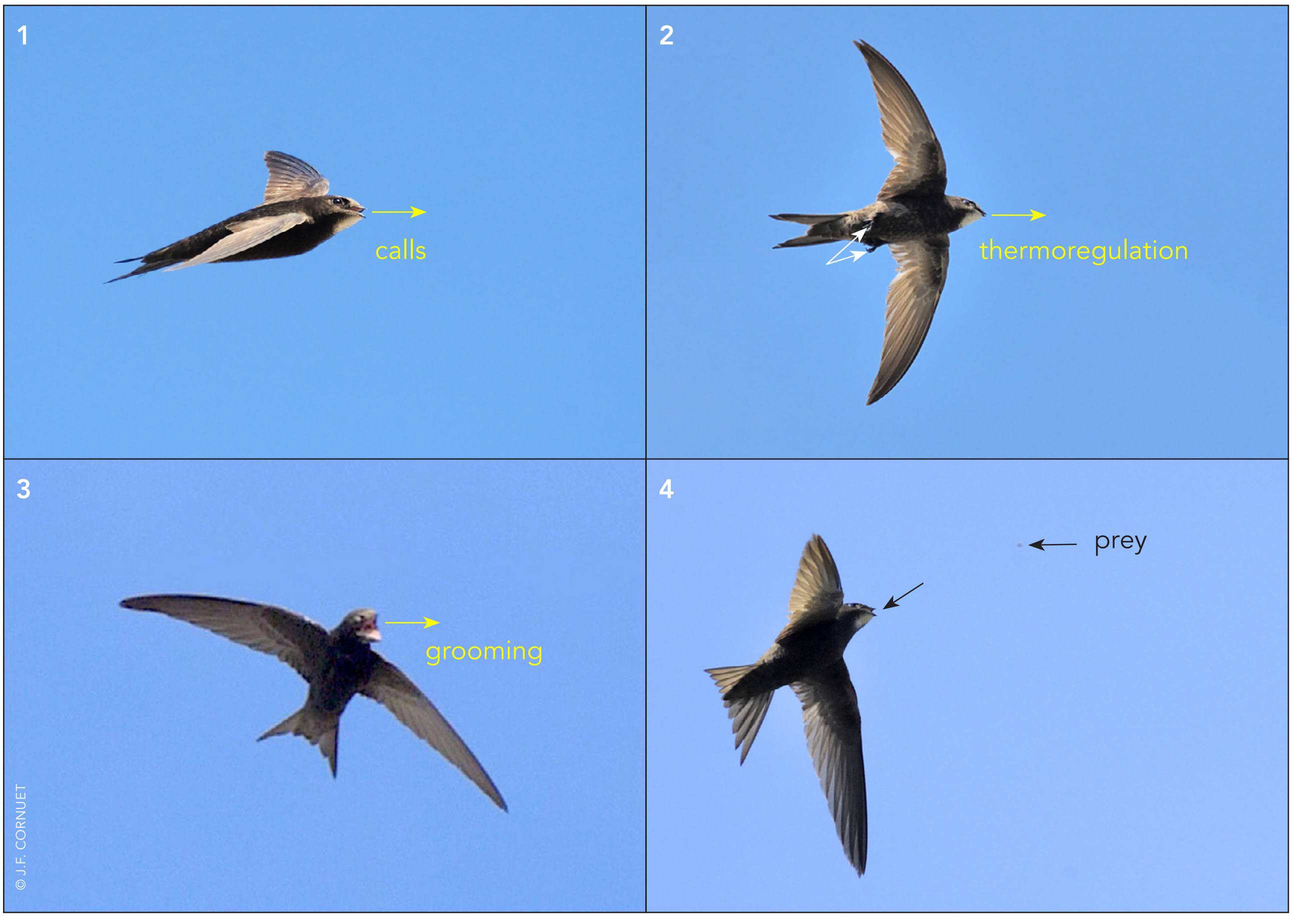


Figure 12.
Beak opening: 1. screaming, 2. thermoregulation, 3. grooming, 4. prey capture

If the Common Swift forages with its beak open, it would face too many problems that could not be solved:

- reduced aerodynamics;
- drying out of the mouth cavity;
- ingestion of hazardous airborne particles;
- visibility, because flying with the beak wide open would interfere with forward visibility.

These problems are common to all birds, so it is safe to say, until proven otherwise, that no bird hunts prey in flight with its beak wide open, neither Nightjars nor any species of Swifts and Swallows. These birds have nerve and muscle structures with very short latency and reaction times that allow them to open and close their beaks with each capture.

4.C.2. Average duration of the beak opening and closing

Out of 1200 captures:

- the average beak opening time is 0.0214 s, with a maximum of 0.0666 s and a minimum of 0.0111 s;
- the average duration of beak closure is 0.0113 s, with a maximum of 0.0277 s and a minimum of 0.0055 s.

The average duration of the opening-closing cycle of the beak is 0.0327 s.

This is an extremely short duration (Figure 13).

The gap opening is variable in size, but sometimes maximum to ensure capture (Figure 7).

Figure 13.
Sequence of all images of a visible prey capture at 180 fps.

Vidéo

4.D. Captures with visible prey

Of the 1200 captures, 120 of them (10 %) show the prey in the time before it disappears in the swift's beak. This prey usually appears in the form of a small blurred spot, white or black, whose path can be followed frame by frame to the bird's beak. Sometimes, under good conditions, a winged insect can be recognized. The swift's prey average size is between 2 and 10 mm. It is therefore not very surprising that they are only seen in good conditions: "large" prey size, good sharpness adjustment of the video, shooting proximity, sky brightness and colour...

4.D.1. Capture success

These 120 captures are all successful: the prey finishes its path well in the swift's beak. The Common Swift appears to be a very efficient hunter and we can assume that the very large majority of the other captures where the prey is not visible are successful.

4.D.2. Swift speed at capture time

Of these 120 captures, 52 allowed the speed to be calculated when the distance separating swift from its prey reduced. According to the videos, the initial or maximum distance between the bird and its prey is between 0.392 m and 1.743 m (Figure 14). **Over these distances the average speed is 7.9 m/s (n = 52).** Considering the speed of the prey insignificant compared to that of the bird, this value can be similar to the ave-

Figure 14.
Distance measurements for calculating the bird's speed (bird's length = 16 cm)

Vidéo

rage speed of the swift's flight. Tunnel and field measurements of the hunting flight give values between 8 and 10 m/s (Henningsson *et al.* 2010). So the average speed of 7.9 m/s is quite consistent. Its value, slightly lower than the data in the literature, can be explained by a calculation made on the last decimetres before capture, which may be marked by a slight slowing of the flight.

4.D.3. Distance from prey to beak when swift begins to open it

Frame-by-frame analysis is used to calculate the distance from beak to prey at the exact moment the beak begins to open (**Figure 14**). Of the 52 captures selected, this distance averaged 17 cm. At a speed of 7.9 m/s, the 17 cm are travelled in 0.0215 s. So the Common Swift opens its beak at the very last moment, which is consistent with the short opening-closing cycle of the beak (0.03 s) and illustrates once again the very efficient neuromuscular abilities of this bird.
Note in passing that 17 cm is within one centimetre of the average length of the Common Swift from the point of the beak to the tip of the tail (16 cm).

4.D.4. Prey selection

Common Swift is considered as prey selector: in the case of bees, they would avoid capturing workers because of the risk of venom injected by their sting, but they would catch the drones that lack it (Lack, 1956). Similarly, it captures harmless hoverflies that look like more dangerous insects such as wasps (aposematism).
Only five of my videos give some ideas on this problem of prey selection. They show two possibilities.

4.D.4.1. Selection by giving up at the last moment before capture

Two videos show the Common Swift can give up a capture at the last minute. The swift is about to capture a prey item that will pass within its range. But at the very last moment, it gives up the capture and lets the insect go (**Figures 15 and 16**).
In both cases, the prey looks like a Hymenoptera that could be dangerous. The danger perception may be visual and/or auditive (sound emissions produced by the insect). It is noted that the giving up is done at the very last moment as if the proximity of the prey was necessary? Does the Common Swift trust the speed of its reactions or does it detect the prey's dangerousness only if it is very close?

Example 1 (**Figure 15**): the video was shot on May 12, the first day of shooting in 2019 with the arrival of the first local breeders. It is therefore most likely a breeding adult of at least 4 years old.

Example 2 (**Figure 16**): the video was shot on June 14, 2019. At this date the chicks are all still in the nest, so it can only be at least one year old experienced individual (yearling) who has captured well over one million prey since birth.

4.D.4.2. Prey selection by immediate discarding after capture

Two other videos nuance swifts' ability to detect potentially risky prey prior to capture.
Both show a swift that has just captured a prey and immediately rejects it vigorously by shaking its head with its mouth wide open (**Figures 17 and 18**).
What can trigger this rejection?
Is it a sting? Could the captured prey have begun to sting the oral mucosa?

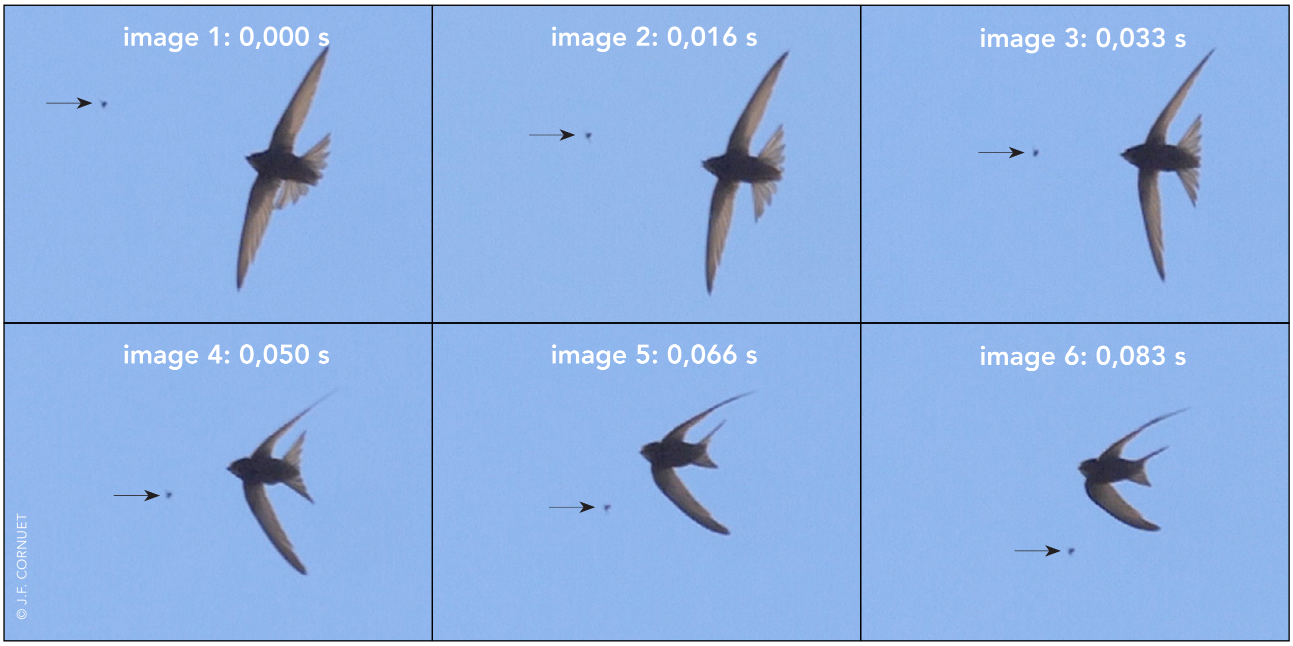


Figure 15.
Example 1: Prey passes within range of the bird. It half opens its beak (image 2), but closes it immediately and gives up the capture (images 4, 5 and 6).

Vidéo

Figure 16.
Example 2: Prey passes within range of the bird (image 4).
It gives up the capture (image 5).

Vidéo

Is it a substance that is perceived as unpleasant or toxic? Does the captured prey have a natural bad taste or is it caused by an allomone-like defence secretion at capture time (Pavis, 1987)
For a long time we thought that birds had no taste sense. But we now know that some species have taste buds that are sensitive to the same four flavours that we have (sweet, salty, bitter and sour) (Birkhead, 2012).

Example 3 (**Figure 17**): the video was shot on June 3, 2018. On this date, it is too early to be a fledgling. It is at least one year old.

Example 4 (**Figure 18**): the video was shot on July 5, 2019. At this date juveniles may start to leave their nest, but the video does not show the typical features of this age (white chin and forehead, lighter overall hue, and pale rims of the feathers and rectrices). The bird also shows moulting feathers on both wings. Like the previous one, it is at least one year old.
An experienced Common Swift can therefore make "distant recognition errors".

The distinction of the most dangerous insects (worker bee...) is perhaps innate. But for other prey, there would be a kind of learning by error without risk (?) for the individual with a selection after capture. Let us note the scarcity of these observations (2 rejections out of 1200 captures) but which is perhaps also linked to a very low abundance of risk insects in the studied site.

4.D.4.3. Failed capture or late selection in extremis?

Example 5 (**Figure 19**): the video shot on 16 May 2019 is problematic to interpret. It is a long sequence of 48 s in real time where the same individual on foraging is filmed.
It is an experienced breeding adult of at least 4 years old, returning from migration a few days earlier.
Initially, 12 successive captures are identified in this video. But the fine analysis of the 11th capture shows visible prey. The bird locates it, modifies its path, projects body and head, beak wide open almost in contact (**Figure 19, image 2**), but the prey is not captured and continues its flight (**Figure 19, image 3**) !

Hypothesis 1: the maximum extension movement is not enough to within a few millimetres, but then why doesn't this swift try a second time, since the prey remains within its reach?
Or does it consider it a failure that does not "deserve" a second attempt?
In fact, it will make a 12th capture of another prey less than 3 seconds later.

Hypothesis 2: did swift, in extremis, identify high-risk prey and therefore give up capturing it?

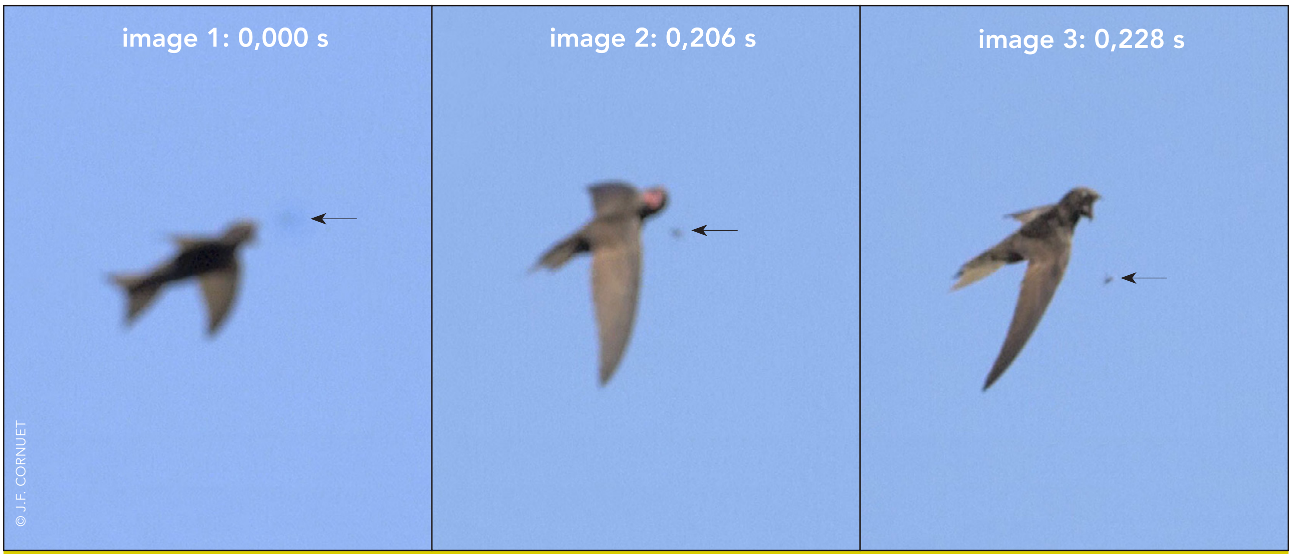


Figure 17.
Example 3: the swift rejects the prey immediately after capture.

Vidéo

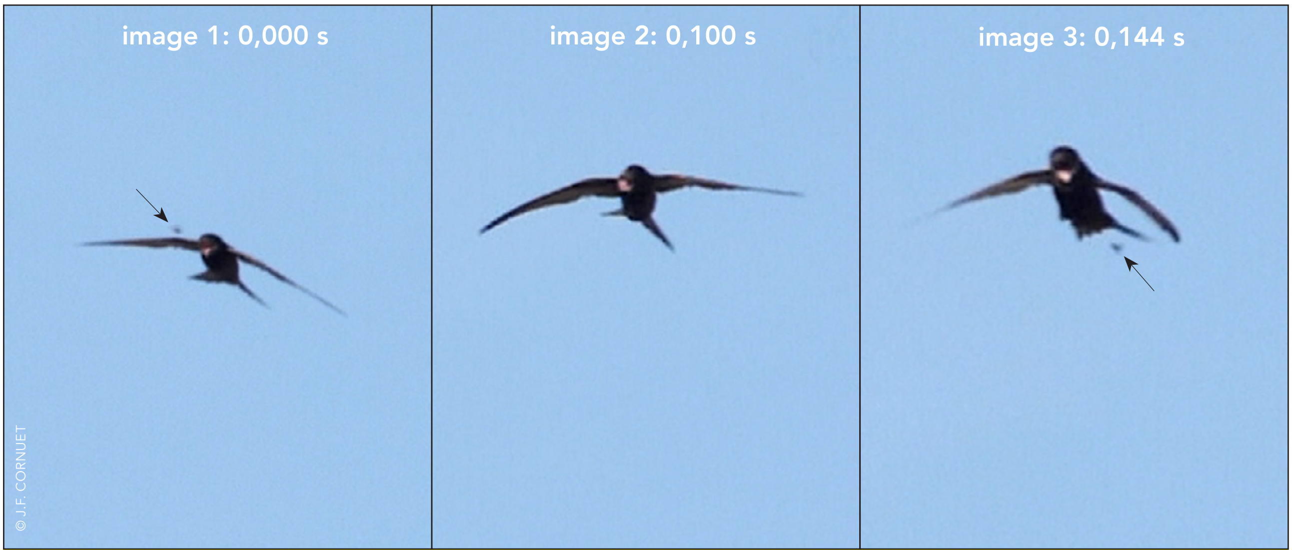


Figure 18.
Example 4: the swift rejects the prey immediately after capture.

Vidéo

Figure 19.
Example 5: the swift fails or gives up the capture.

Vidéo

5. Flights, paths and postures just after capture

Just prior to capture, swifts are mostly in «horizontal» or ascending flapping flight (81 %) than in gliding flight (19 %) (**Table 3**)

After capture, the percentages equalize: 50 % in flapping flight and 50 % in gliding flight.

Comparison between flights before and after capture shows that:

- **60 % of the individuals keep the same type of flight:**
  - **45 % stay in flapping flight;**
  - **15 % stay in gliding flight.**
- **40 % of individuals change flight type:**
  - **36 % switch from flapping to gliding;**
  - **4 % switch from gliding to flapping.**

Prey capture thus induces for 40 % of the captures a change in the flight type, with a strong tendency for switch from flapping to gliding.

Considering only gliding after capture (n = 608) 64 % of gliding is done with a turn as if the bird was trying not to go too far away from an area that may be good for other captures.

This turn following capture helps to keep the bird in an area with potential prey and explains the sinuous or tortuous path highlighted in the 3D representations (De Margerie, 2018).

6. Time intervals between 2 consecutive captures

In a sample of 21 videos, with 6 to 15 captures (190 captures), there are 169 time intervals between 2 consecutive captures. The average duration of the time interval between two successive captures is 3.00 seconds.

For example, **Figure 20** shows 14 captures made in 39 s by a swift, that is one capture every 3.00 s.

- **The shortest interval is 0.581 s between captures 12 and 13.**
- **The longest interval is 6.206 s between captures 8 and 9.**

In all my videos, the "shortest interval record" is held by an individual with a bolus that sequences 3 successive captures in 0.532 s with equal intervals of 0.266 s between each capture (**Figure 22**).

In the literature, the Common Swift is supposed to capture a prey item approximately every five seconds (Elkins, 2010). This average value is based on an unspecified calculation (Simpson, 1967) that appears to be related to data on the number of prey found in boluses and the time taken to collect them (Lack, 1956).

Thus with a diet of small prey, the Common Swift is forced to devote most of its time to finding insects. During the breeding season, this requirement increases while the chicks are being fed.

So the values found in my calculations confirm the Common Swift's amazing ability to collect prey very quickly.

Figure 20.
14 captures in 39 seconds, i.e. an average of one capture every 3.00 seconds.

Vidéo

7. The special case of bolus captures

7.A. Bolus

A bolus is a hazelnut-sized food ball (1 to 1.5 cm in diameter) weighing 1 to 2 g on average, made up of prey that may still be alive and stuck together by the bird's slimy saliva. Observed only in adults at the breeding-time, it is the visible sign that hatching has taken place and that the chicks have started to be fed. The hunting adult does not swallow prey intended for chicks but accumulates it in its oral cavity, whose elastic floor distends and deforms as prey items are caught (**Figure 21**).
The swift has no particular organ for storing prey. It is best to avoid using the term "sublingual pouch" (as I did in Part 1 of this paper). True sublingual pouches exist in some species of birds such as the Rosy Finch *(Leucosticte tephrocotis)* (Miller, 1941).
In the swift, it's the floor of the mouth cavity that expands.
We can make two hypotheses.
At the breeding time, under hormonal action:

- hypothesis 1: saliva secretion would increase to stick the nest materials together and gather food ball (bolus);
- hypothesis 2: the skin elasticity of the mouth floor would increase as the chicks hatch.

The growth rate of the bolus depends on prey availability and size. In good warm weather, with a "normal" abundance of prey, a swift takes 45 to 60 min to build a bolus with 300 to 1000 prey (Lack, 1956). It takes much longer when the weather conditions are bad (rain, cold, wind...).

Figure 21.
Common Swift with mouth cavity distended by the bolus

The adult's return to the nest must be caused by a critical volume of the bolus perceived by the distension of the skin on the floor of the oral cavity.
In the early days, adults share the bolus between the chicks. But soon chicks are able to ingest the entire bolus.

7.B. Number of captures with bolus

Of the 1200 captures, only 34 are made by individuals with a bolus:

- 2017: 10 captures with bolus from 10 June to 22 June;
- 2018: 8 captures with bolus from 22 June to 19 July;
- 2019: 16 captures with bolus from 27 June to 25 July.

This low proportion (2.8%) of bolus captures may have several explanations.

- The low number of breeding pairs at the station was estimated at only 5 breeding pairs.
- Breeders do not present a bolus until after the chicks hatch at the earliest at the end of the first 10 days of June.
- Adults in charge of chicks may choose other foraging areas that are richer in prey than the vicinity of the colony where they would make their last captures before going to the nest.

This last hypothesis is in agreement with the observation that the majority of adults filmed carry a bolus close to its maximum size.

7.C. Capture postures with bolus

7.C.1. Comparison of captures with and without bolus

On this small sample of bolus captures (n = 34), there do not seem to be any significant differences with other captures (**Tables 5 and 6**).

Captures with bolus show 3 slight tendencies (**Table 5**):

- before capture: a higher frequency of gliding compared to flapping;
- capture: a lower frequency of head projections;
- after capture: a higher frequency of gliding compared to flapping.

In the detail of the combinations (**Table 6**) it is difficult to establish real tendencies because of the small size of the data.

The presence of a bolus in the oral cavity, after a few tens of minutes, tends to make the bird 1 to 2 g heavier, with the following consequences:

- the forward shift of its center of gravity;

Table 5.
Impact of the bolus on flight patterns and head postures

		CAPTURE WITHOUT BOLUS	CAPTURE WITH BOLUS
Captures number (n = 1200)		1 166	34
Flight before capture	Flapping	82 %	71 %
	Gliding	18 %	29 %
Head posture	"Projected"	78 %	74 %
	"Retracted"	22 %	26 %
Flight after capture	Flapping	50 %	54 %
	Gliding	50 %	46 %

Table 6.
Impact of bolus on the distribution of the 18 combinations of the 8 types of flight and postures before, during and after capture

Flight before capture - Head Flight after capture	Number of captures without bolus	Number of captures with bolus
1. Ascending flapping flight - "Projected" head Gliding flight with a turn	276 (23,7 %)	3 (8,6 %)
2. "Horizontal" flapping flight - "Projected" head Flapping flight	217 (18,6 %)	3 (8,6 %)
3. Ascending flapping flight - "Projected" head Flapping flight	173 (14,8 %)	8 (22,9 %)
4. "Horizontal" flapping flight - "Retracted" head Flapping flight	120 (10,3 %)	3 (8,6 %)
5. Gliding flight - "Projected" head Gliding flight	82 (7,0 %)	5 (14,3 %)
6. "Horizontal" flapping flight - "Projected" head Gliding flight	40 (3,4 %)	2 (5,7 %)
7. Gliding flight - "Retracted" head Gliding flight	37 (3,2 %)	3 (8,6 %)
8. Gliding flight - "Projected" head Gliding flight with a turn	34 (2,9 %)	1 (2,8 %)
9. Gliding flight - "Projected" head Flapping flight	32 (2,7 %)	
10. "Horizontal" flapping flight - "Projected" head Gliding flight with a turn	32 (2,7 %)	
11. Ascending flapping flight - "Projected" head Gliding flight	27 (2,3 %)	4 (11,4 %)
12. Ascending flapping flight - "Retracted" head Flapping flight	20 (1,7 %)	1 (2,8 %)
13. "Horizontal" flapping flight - "Retracted head Gliding flight with a turn	15 (1,3 %)	1 (2,8 %)
14. "Horizontal" flapping flight- "Retracted" head Gliding flight	16 (1,4 %)	
15. Gliding flight - "Retracted" head Gliding flight with a turn	15 (1,3 %)	
16. Gliding flight - "Retracted" head Flapping flight	14 (1,2 %)	1 (2,8 %)
17. Ascending flapping flight - "Retracted" head Gliding flight with a turn	11 (0,9 %)	
18. Ascending flapping flight - "Retracted" head Gliding flight	4 (0,3 %)	
Total	**1 165**	**35**

- **the possible reduction of the beak opening amplitude.**

We can therefore assume that the presence of a bolus before returning to the nest can progressively modify the capture technique during the collection of prey, for example by reducing acrobatic postures with body extension and strong head projection.

7.C.2. Head projection with bolus

The proportions have been maintained (Table 7). In detail, the presence of a bolus seems to reduce projection amplitude somewhat due to the increase in head mass when the bolus reaches its almost maximum size.

7.C.3. Beak opening and closing in captures with bolus

A bolus (Table 8) increases the average duration of:

- beak opening by 7 %;
- beak closure by 30 %;
- open-close beak by 15 %.

A bolus seems to slow down the beak closure most of all. This is what you would expect due to the bolus size in the mouth cavity.

But we must put this result into perspective because the variations are at the level of thousandths of a second and concern only 34 catches over 1200.

7.C.4. Captures with bolus where prey is visible

Of the 1200 catches, prey is visible on 120 of them (10 %). Calculations could be made on a sample of 52 captures with only 3 captures with a bolus.

A bolus does not seem to have a significant impact on the 2 calculated parameters (Table 9).

7.C.5. Time intervals between 2 consecutive catches with bolus

Of the 34 bolus captures, 16 are part of a chain of successive captures:

- 5 sequences of 2 captures;
- 2 sequences of 3 captures.

The average duration of the 9 intervals

Table 7.
Impact of a bolus on flight types and head postures

	CAPTURE WITHOUT BOLUS	CAPTURE WITH BOLUS
Captures number	914	25
Head forward projection	43,5 %	40, 0 %
Head upward projection	29,6 %	32,0 %
Head sideward projection	26,1 %	24,0 %s
Head downpward projection	0,8 %	4,0 %

Table 8.
Impact of a bolus on average beak opening and closing times

	CAPTURE WITHOUT BOLUS	CAPTURE WITH BOLUS
Captures number	1166	34
Beak opening	0,0213 s	0,0229 s
Beak closing	0,0112 s	0,0146 s
Beak opening + closing	0,0325 s	0,0375 s

Table 9.
Impact of a bolus on a swift's speed and distance from the prey when it starts to open its beak (captures with visible prey).

	CAPTURE WITHOUT BOLUS	CAPTURE WITH BOLUS
Captures number	49	3
Average swift speed	7,9 m/s	7,2 m/s
Average distance beak opening	17 cm	15,5 cm

between 2 successive captures with boluses is 1.8 s.

Hunting with a bolus does not reduce the ability to chain captures with time intervals of 1 to 2 seconds.

On the opposite, one video shows that a swift with bolus is able to make 3 successive captures in a time interval of 0.532 s with equal intervals of 0.266 s between each capture (**Figure 22**).

This high frequency of captures is necessary to ensure the chicks' feeding without forgetting that parents also have to provide for their food needs.

Review
Carrying the food ball (bolus) in the mouth appears to have little impact on the swift's ability to catch prey.

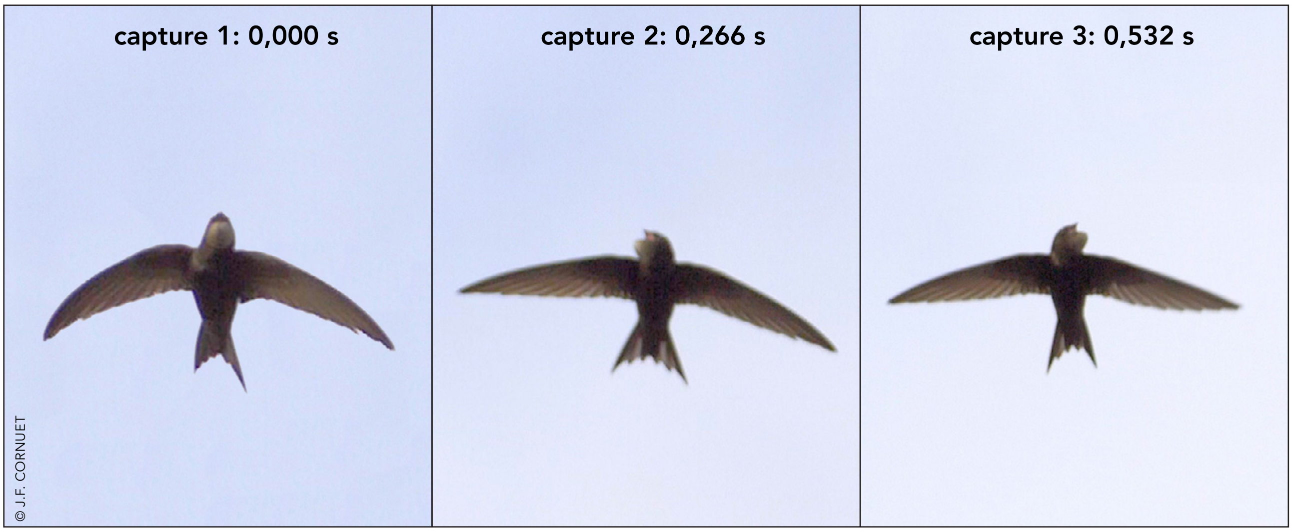


Figure 22.
Common Swift with a bolus making 3 successive captures in 0.532 s
Vidéo

8. Comparison between two foraging stations

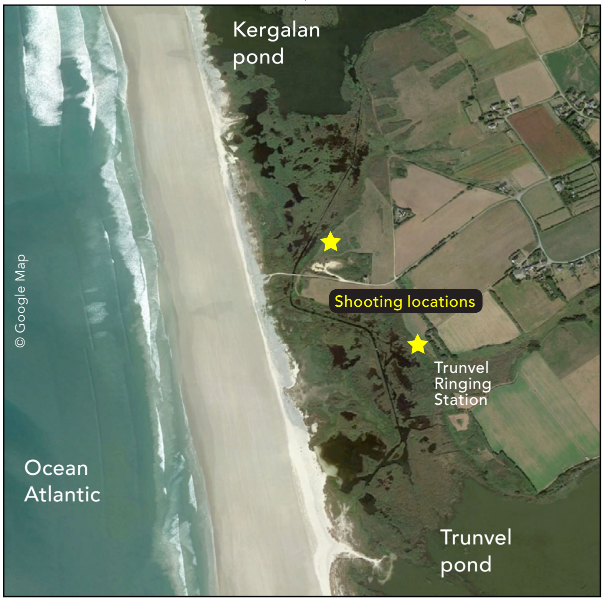
At the end of April - beginning of May 2019, I filmed swifts migrating over coastal marshes in Bretagne (France). For me it seemed interesting to compare the feeding habits of these birds on the 2 stations that will be named:

- migration-station;
- breeding-station.

8.A. Shooting conditions

In the **breeding-station**, 111 days from the beginning of May to the end of July in 2017, 2018 and 2019 were devoted to shooting over suburban residential area in the suburbs of Paris in the Île-de-France (**Figure 23, right**). Approximately 4 to 5 pairs make up a small urban colony of birds nesting under rooftops. To these breeding adults are added in successive waves of young nesting, pre-nesting and first-year immature birds, according to a complex schedule of departures and arrivals (Genton, 2016) from May to July.
All these individuals forage over pavilions and buildings with gardens, mainly between 6:00 and 11:00 am.
The shots are taken from the roof of my pavilion at a height of 10 m, with the filmed birds moving between 10 and 30 m above the ground.
Swifts are only visible on the site in good weather, with blue or foggy skies and especially without wind.
Over the 3 years, 1200 captures were identified out of the thousands of videos recorded.

In the **migration-station**, 4 days (28 April, 2,3 and 4 May 2019) were devoted to video recording swifts over coastal marshes in the commune of Tréogat in the Bay of Audierne in Bretagne (**Figure 23, left**). This site, partially set aside as a reserve (Trunvel-Tréogat Biological Reserve), is an important migratory stopover for many bird species such as the very scarce Aquatic Warbler (*Acrocephalus paludicola*). Each year for the past 31 years, the Trunvel ringing station has been open from mid-July to mid-October to ring birds on post-nuptial migration that are stationed in coastal wetland phragmit groves.
This site also serves as a migratory stopover for Common Swifts on their pre-breeding migration in late April - early May since several thousand individuals are observed there each year. They are all adults, 3-4 years old or more, who come to breed in the urban colonies of Finistère or who will continue their migration further north in the British Isles.
Perhaps they come directly from the north of Spain after crossing the 1000 km of the Bay of Biscay?
During this stopover, they actively forage in this area that is particularly rich in aerial insects.
Shots were taken from the ground between noon and 4:00 pm on birds flying between 1 and 15 m in altitude. Depending on the day and time of day, the sky was blue or overcast but with no rain.
An important weather element was the erratic north wind, which conditioned the swift's aerial movements over the reed beds.
In 4 days, 234 captures could be filmed.



MIGRATION-STATION
Audierne bay
Bretagne

BREEDING-STATION
Paris suburb
Île-de-France

Common swifts foraging above
coastal reedbeds

Common Swifts foraging over
the roofs of pavilions

Figure 23.
Geographic location and foraging areas overviews at the two stations

8.B. Foraging flight

In the **breeding-station**, foraging flight is a tortuous flight with a sinuous path where the bird follows a series of captures by describing loops with many turns.

The average duration of flapping flight bouts is 1.0 s. The average duration of gliding bouts is 1.4 s.

In fine weather, hot, windless, Common Swift forages by spending on average more time gliding than flapping. But the proportions of the two types of flight can vary greatly depending on the weather conditions.

In the **migration-station**, in fine weather with a light wind, the foraging flight looks like the one at the breeding-station.
But when the wind blows regularly in one direction, the swifts fly lower, sometimes at the reedbed level where they fly in a sort of elliptical path (**Figure 24**).

They allow themselves to be carried in gliding tailwind flight, rarely making captures. Then suddenly they turn to face the wind. They then fly headwind with an energetic flapping flight. This return to the starting point is broken up by sequences of ascending glides that are often used for captures over vegetation.

Then the cycle repeats itself: tailwind gliding flight, 180° turn, headwind flapping flight with ascending glides for catching...
The size of these elliptical circuits varies by a few tens of meters, sometimes more when the bird moves away so that it can no longer be filmed.

The timing of these circuits is likely to depend on the wind regime, catch frequency and local prey abundance.

Figure 24.
Common Swifts flying headwind just above the reedbed

8.C. Flights, paths and postures

8.C.1. Captures after an ascending gliding flight

On the migration-station, a fourth type of flight prior to capture was filmed: the **ascending gliding flight**.

8.C.1.1. Description

When hunting headwind, when prey is detected, the bird glides up to make the capture (**Figure 25**).

The headwind increases lift enough to allow the bird to glide upwards. This is the same principle used by airplanes: facing the wind allows them to take off faster over a shorter distance.

8.C.1.2. Triggering

The ascending gliding flight can be triggered by prey detection. But this is not as clear-cut as for ascending flapping flight, where the limits are more precise. When hunting headwind, swift may rise in glide, but not always to make a capture. This also allows it to explore the air layer above the reedbed.

8.C.1.3. Path

The ascending angle of this glide produced by the headwind has a small to moderate variable amplitude that the bird adjusts with wings and tail.

8.C.1.4. Average duration

The analysis of 24 ascending glides gives an average duration of 0.46 s from trigger to capture.
This is less than the average duration of the ascending flapping flight (0.78 s).

But unlike the ascending flapping flight, the progress of the ascending glide is directly related to the characteristics of the wind (speed, direction...).
Therefore, it can be hypothesized that the ascending flapping flight, in calm, windless weather, has a more constant pattern and average duration than the ascending gliding flight.

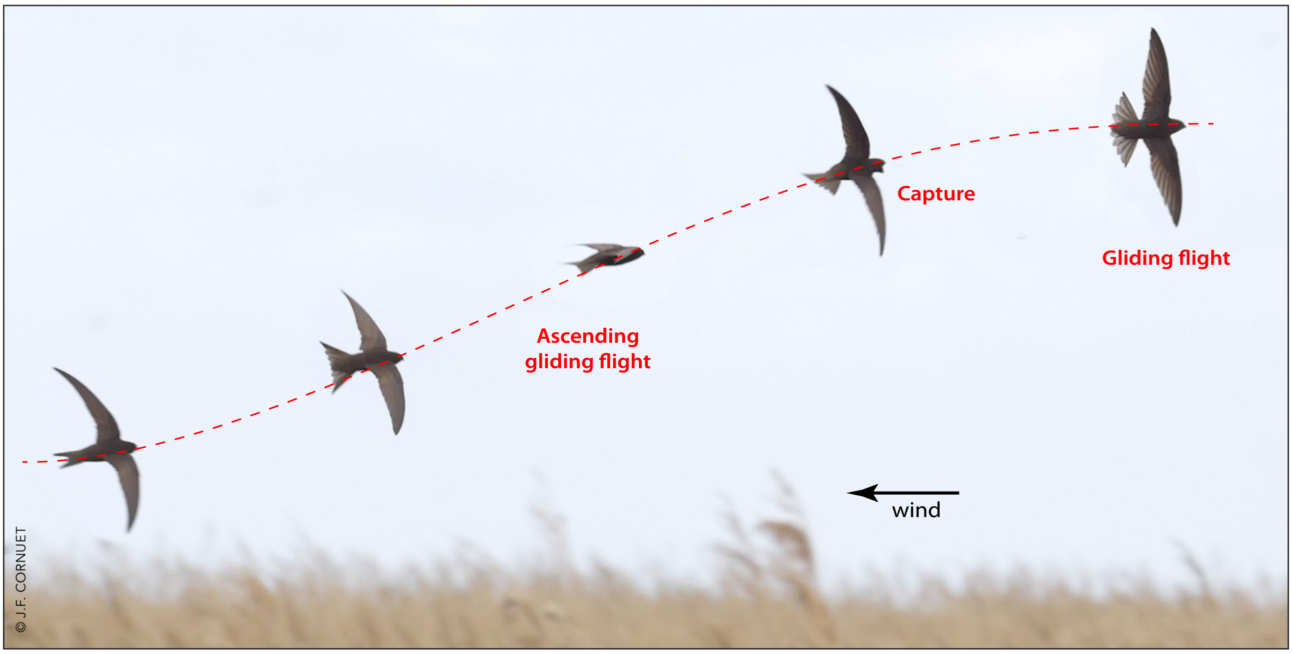


Figure 25.
Capture path with ascending gliding flight – "projected" head – gliding flight
Vidéo

The ascending glide now leads to consider 24 combinations. But some of them are not represented in the 2 stations, so they have not been included in the comparative table (Table 10).

Table 10.
Comparison of flights, paths and postures distribution between both stations

Flight before capture - Head Flight after capture	BREEDING-STATION	MIGRATION-STATION
Ascending flapping flight - "Projected" head Gliding flight with a turn	279 (23,25 %)	15 (6,41 %)
"Horizontal" flapping flight - "Projected" head Flapping flight	220 (18,33 %)	60 (25,64 %)
Ascending flapping flight - "Projected" head Flapping flight	181 (15,08 %)	10 (4,27 %)
"Horizontal" flapping flight - "Retracted" head Flapping flight	123 (10,25 %)	10 (4,27 %)
Gliding flight - "Projected" head Gliding flight	87 (7,25 %)	38 (16,24 %)
"Horizontal" flapping flight - "Projected" head Gliding flight	42 (3,50 %)	11 (4,70 %)
Gliding flight - "Retracted" head Gliding flight	40 (3,33 %)	1 (0,43 %)
Gliding flight - "Projected" head Gliding flight with a turn	35 (2,92 %)	11 (4,70 %)
Gliding flight - "Projected" head Flapping flight	32 (2,66 %)	13 (5,55 %)
"Horizontal" flapping flight - "Projected" head Gliding flight with a turn	32 (2,66 %)	16 (6,84 %)
Ascending flapping flight - "Projected" head Gliding fligh	31 (2,58 %)	11 (4,70 %)
Ascending flapping flight - "Retracted" head Flapping flight	21 (1,75 %)	1 (0,43 %)
"Horizontal" flapping flight - "Retracted" head Gliding flight with a turn	16 (1,33 %)	1 (0,43 %)
"Horizontal" flapping flight- "Retracted" head Gliding flight	16 (1,33 %)	1 (0,43 %)
Gliding flight - "Retracted" head Gliding flight with a turn	15 (1,25 %)	
Gliding flight - "Retracted" head Flapping flight	15 (1,25 %)	7 (3,00 %)
Ascending flapping flight - "Retracted" head Gliding flight with a turn	11 (0,92 %)	1 (0,43 %)
Ascending flapping flight - "Retracted" head Gliding flight	4 (0,33 %)	
Ascending gliding flight - "Projected" head Flapping flight		**7 (3,00 %)**
Ascending gliding flight - "Projected" head Gliding flight		**13 (5,55 %)**
Ascending gliding flight - "Projected" head Gliding flight with a turn		**7 (3,00 %)**
Total	1200	234

8.C.2. Comparison of flights, paths and postures distribution between the 2 stations (Table 10)

8.C.2.1. Prior to capture

On the breeding-station:

- 81 % of the birds are in flapping flight;
- 19 % are in gliding flight.

On the migration-station:

- 58 % of the birds are in flapping flight;
- 42 % are in gliding flight.

On the migration-station, the wind allows swifts to use gliding more often, which is less costly in terms of energy costs.

8.C.2.2. Captures

On the breeding-station:

- 78 % of captures are made with a head projection;
- 22 % of captures are made without head projection.

On the migration-station:

- 91 % of captures are made with a head projection;
- 9 % of captures are made without head projection.

The higher frequency of captures with head projection at the migration-station can be explained by:

- more turbulent air (winds);
- faster hunting speed;
- larger prey.

8.C.2.3. After capture

On the breeding-station:

- 50 % of the birds are in flapping flight;
- 50 % are in gliding flight.

On the migration-station:

- 46 % of the birds are in flapping flight;
- 54 % are in gliding flight.

In both stations, the two types of flight have roughly balanced frequencies. In detail, by considering only gliding, differences appear.

On the breeding-station:

- 64 % of the captures are followed by a glide with a turn;
- 36 % of the captures are followed by a glide without turn.

On the migration-station:

- 42 % of the captures are followed by a glide with a turn;
- 58 % of the captures are followed by a glide without turn.

In the **breeding-station**, in windless weather, the turns following the captures are interpreted as flight manoeuvres aimed at exploiting a hunting area with potential prey through a sinuous path.

In the **migration-station**, above the reedbeds, swifts make hunting tracks according to the wind regime: hunting by flying with the headwind, then fast return with tailwind to start again for a hunting flight with the headwind. These circuits explain the lower frequency of captures followed by a glide with a turn.

Note: If no ascending glides were observed at the breeding-station, it is because the birds only hunted on the site during calm, windless weather.

8.C.3. Head postures

At both stations, head projections at the capture time are mainly forward, in the direction of the bird's flight (**Table 11**).
The high percentage of head-up projections compared to the very low percentage of head-down projections strengthen the already developed idea that swifts do not dive on their prey but prefer to capture it from below.

8.C.4. Captures in inverted flight

In the breeding-station, out of the 1200 captures, 46 (3.8 %) of them show a inverted flight:

- 22 take place in an inverted flight;
- 24 captures are followed immediately by an inverted flight.

In the migration-station, out of the 234 catches, 11 (4,7 %) of them show a inverted flight (**Figure 26**):

- 6 captures take place in an inverted flight;
- 5 captures are followed by an inverted flight.

Table 11.
Distribution of the 4 directions of the head's "projection" in both stations

	BREEDING-STATION	MIGRATION-STATION
Head forward projection	409 (43,5 %)	104 (49 %)
Head upward projection	278 (29,6 %)	74 (35 %)
Head sideward projection	245 (26,1 %)	28 (13 %)
Head downpward projection	7 (0,8 %)	6 (3%)
Captures with projection	**939**	**212**

Figure 26.
Inverted flight capture over the reedbed

Vidéo

8.D. Beak opening and closing

In the both stations, the average beak opening and closing durations are very similar: the differences start only to the thousandth of a second (**Table 12**).
The very slightly higher values at the migration-station can be explained by the slightly higher flight speed and prey size at this station.

For example, the capture of a Zygoptera Odonata (**Figure 27**) required some head contortions to fully ingest this fine but long prey [average length: 30 mm in the blue-tailed Damselfly (*Ischnura elegans*) observed at the site on the same day].

Table 12.
Average beak opening and closing durations in both stations

		BREEDING-STATION	MIGRATION-STATION
Captures number		1200	234
Beak opening	Minimum value	0,0111 s	0,0166 s
	Average duration	**0,0214 s**	**0,0250 s**
	Maximum value	0,0666 s	0,0555 s
Beak closing	Minimum value	0,0055 s	0,0083 s
	Average duration	**0,0113 s**	**0,0111 s**
	Maximum value	0,0277 s	0,0166 s
Opening + Closing	Minimum value	0,0166 s	0,0277 s
	Average duration	**0,0327 s**	**0,0400 s**
	Maximum value	0,0833 s	0,0722 s

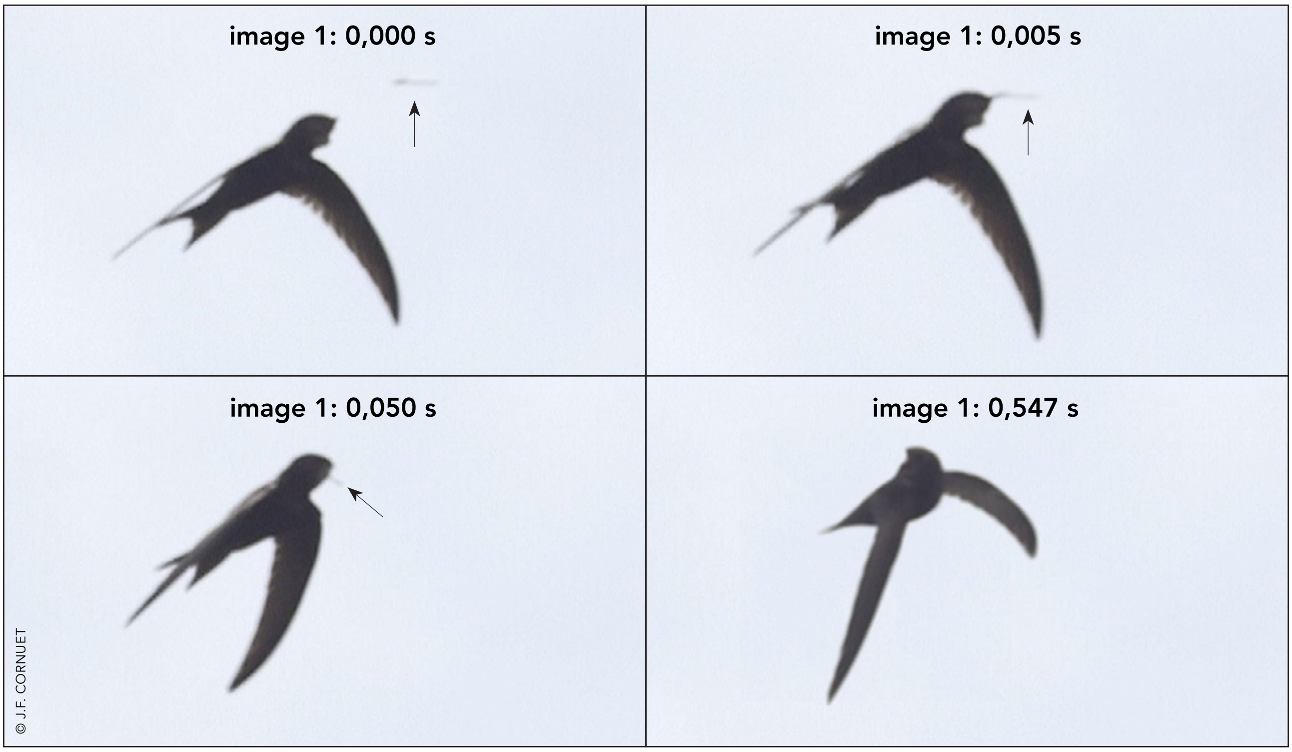


Figure 27.
"Longer" swallowing of a Zygoptera Odonata requiring head contortions

8.E. Captures with visible prey

8.E.1. Captures number

In the breeding-station, prey is visible in only 10 % of the captures, whereas in the migration-station this percentage is 73 % (Table 13). The different shooting conditions, especially the distance to the filmed bird, do not seem to be an explanatory factor because the swifts size varies in the same proportions in the videos filmed at the both stations.

The most likely explanation is the higher average prey size at the migration-station. To simplify, it can be considered that the majority of prey at the breeding-station had to be smaller than 5 mm (arbitrary value) while those at the migration-station had to be larger than 5 mm.

8.E.2. Capture success

As already noted in the breeding-station, the 172 captures with visible prey made in the migration-station were all successful: the prey finishes its path well in the swift's beak. This result confirms what we wrote for the breeding-station: the Common Swift is a very efficient hunter and we can assume that the vast majority of the other captures where the prey is not visible are successful.

8.E.3. Swift's speed at capture time

At both stations, on samples of 52 and 57 captures respectively, it was possible to calculate the mean swift speed just prior to capture (Table 13). It was 9.8 m/s at the migration-station. This value is 24% higher than that found at the breeding-station (7.9 m/s).

This faster foraging flight has to be related to a lower flight altitude over the reed bed, larger prey with faster movements, more wind-swept air and hungrier adult migrants.

8.E.4. Distance from prey to beak when swift begins to open it

The mean distance from prey to beak (Table 13) when it begins to open is 47% greater in the migration-station (25 cm) than in the breeding -station (17 cm). Faster flying speed at the migration-station may account for this difference.

Table 13.
Captures where prey is visible in both stations

	BREEDING-STATION	MIGRATION-STATION
Total number of captures	**1200**	**234**
Number of captures with visible prey	120 (10 %)	172 (73 %)
Number of captures with visible prey allowing calculations	52	57
Average speed of swift at the capture time	7,9 m/s	9,8 m/s
Average distance from prey to beak when beak begins to open	17 cm	25 cm

8.F. Time intervals between 2 consecutive captures

At both stations, a sample of active-hunting videos with multiple captures was compared (**Table 14**).
The shortest interval between two captures and the average length of the intervals have close values.
However, these two parameters are slightly higher at the migration-station in correlation with a faster foraging flight to capture larger prey with faster movements in more windy air.
Figure 28 shows the example of swift making 9 successive captures in 35,5 s at the migration-station. The average time interval between 2 captures is 4,4 s.

Table 14.
Time intervals between captures in the both stations

	BREEDING-STATION	MIGRATION-STATION
Number of videos with multiple captures	21	15
Captures number	190	73
Intervals number between 2 captures	169	58
Shortest interval between 2 captures	0,266 s	0,358 s
Average duration of the intervals between 2 captures	3,0 s	4,0 s

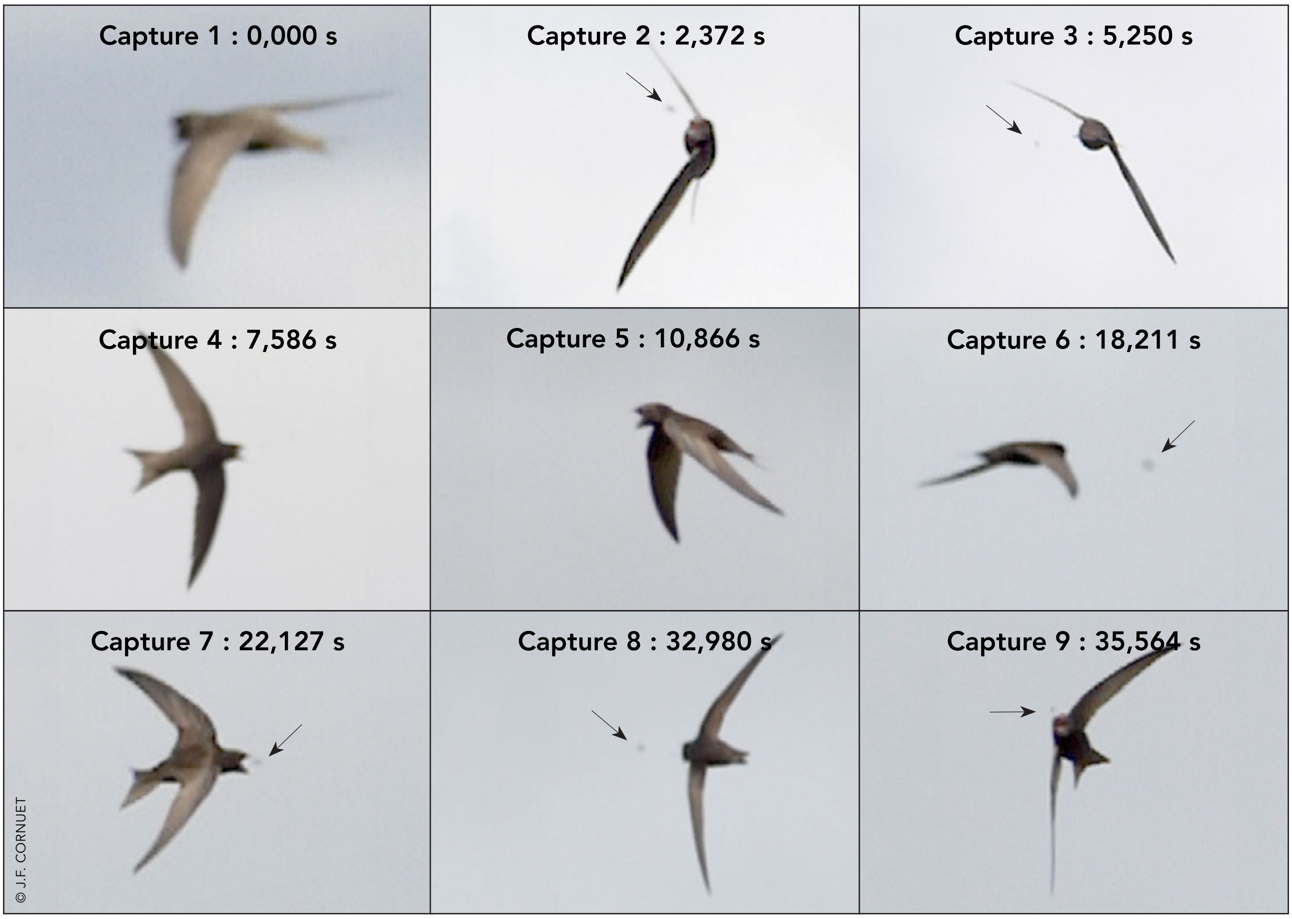


Figure 28.
9 successive captures in 35.5 seconds, i.e. an average interval of 4,4 sec.
Vidéo

8.G. Comparison results

Comparison between breeding-station and migration-station allows a kind of generalization. Indeed, trophic behaviors are very similar, while hunting environment, status and food needs of individuals concerned are different.

In both stations, captures with visible prey (n = 292) are all successful: the Common Swift is a very efficient hunter!

While some of the captures are made discreetly when the bird's path matches that of the prey, most of others are made after a short ascending flapping flight or gliding when the bird hunts headwind.

The head's projection forward, upward or sideways, with or without an overall body projection movement, often contributes to successful capture. The posture adopted at capture time does not necessarily depend on the size of the prey: the bird can vigorously project the body and head, with the beak wide open and eyes half-closed, to capture a tiny prey item!

Whatever the circumstances, swift hunts with closed beak: it opens and closes it on each prey in a very short time of a few hundredths of a second.

If necessary, swift knows how to use inverted flight to ensure the success of certain captures.

During the feeding period, the presence of a bolus in breeding adults does not seem to affect hunting and catching abilities.

The time intervals between captures are counted in seconds, but when prey abondance is hight, they can be very short in the order of a few tenths of a second.

However, time of year, land configuration, availability and size of prey, as well as air mass movements are likely to modify some of the hunting flight features, such as flight height, bird speed, hunting circuit, etc.

9. Comparison with the Alpine Swift

August 16, 2018 and August 22, 2019, near the summit of La Bourgeoise mountain (Samoëns, Haute-Savoie, France), at an altitude of 1760 m, I filmed groups of Alpine Swifts (*Tachymarptis melba*) hunting over grassy ridges. They are birds from local colonies settled in the limestone cliffs of the Haut-Giffre.

9.A. Shooting conditions

Their foraging flight over the site lasted only a few minutes each time:

- between 10:00 and 10:15 am, on August 16, 2018;
- between 01:00 and 01:15 pm on August 22, 2019.

Both days the weather was fine and warm with cloudy sky and light wind. Many insects were present and very active. The weather conditions were particularly good for thermal and orographic updrafts.

On August 16, 2018, 10 videos were shot where 12 captures were identified. On August 22, 2019, 8 videos were filmed where 16 captures were made, half of them by one or more individuals with a bolus.

The 28 captures were analysed with the same methodology used for the Common Swift. Even with this small sample size, it was possible to describe and characterize behaviors common to both species, as was already the case with grooming in Part 1.

However, to be more rigorous, it should be possible to film the two species hunting on the site together in June and July (personal observations).

Alpine Swift foraging over grassy ridges

9.B. Foraging flight

The foraging flight of the Alpine Swift, like that of the Common Swift, is made up of alternating flapping and gliding flight bouts.
The 18 videos represent a total time of 105 s in hunting flight.
Time spent:

- in gliding flight is 81 s (77 %)
- in flapping flight is 24 s (23 %).

These are more or less the same values found for the Common Swift in similar weather conditions (nice warm weather, no wind...).

The average duration of the bouts:

- of gliding flight is 3.0 seconds;
- of flapping flight is 1.5 seconds.

These values are higher than those of Common Swifts (gliding flight: 1.4 s; flapping flight 1.0 s) on the breeding-station. As with grooming, where the mean durations were also higher, these differences can be explained in part by the average dimensions of the two species (Table 15).
With its larger wingspan, the Alpine Swift makes long gliding crossings taking advantage of thermal and orographic updrafts.

Table 15.
Comparison of body measurements between Common Swift and Alpine Swift

	Weight	Length	Wingspan
Common Swift	42 à 48 g	16 à 17 cm	42 à 48 cm
Alpine Swift	80 à 120 g	20 à 22 cm	54 à 60 cm

9.C. Flights, paths and postures

In Alpine Swift, there are 10 of the 18 combinations described for Common Swift (**Table 16**).

Of the 28 captures, 71 % are made after a glide, 64 % are accompanied by a head projection and 79 % are followed by a glide (**Table 17**). This shows the importance of gliding flight before and after capture in Alpine Swift.

In both species, head projection is observed in a large part of the captures.

Table 16.
Comparison of flights, paths and postures distribution between both species

Flight before capture - Head Flight after capture	COMMON SWIFT	ALPINE SWIFT
1. Ascending flapping flight - "Projected" head Gliding flight with a turn	279 (23,25 %)	
2. "Horizontal" flapping flight - "Projected" head Flapping flight	220 (18,33 %)	1 (3,57 %)
3. Ascending flapping flight - "Projected head" Flapping flight	181 (15,08 %)	1 (3,57 %)
4. "Horizontal" flapping flight - "Retracted head" Flapping flight	123 (10,25 %)	2 (7,14 %)
5. Gliding flight - "Projected" head Gliding flight	87 (7,25 %)	11 (39,28 %)
6. "Horizontal" flapping flight - "Projected" head Gliding flight	42 (3,50 %)	1 (3,57 %)
7. Gliding flight - "Retracted head" Gliding flight	40 (3,33 %)	7 (25 %)
8. Gliding flight - "Projected" head Gliding flight with a turn	35 (2,92 %)	
9. Gliding flight - "Projected" head Flapping flight	32 (2,66 %)	1 (3,57 %)
10. "Horizontal" flapping flight - "Projected" head Gliding flight with a turn	32 (2,66 %)	1 (3,57 %)
11. Ascending flapping flight - "Projected" head Gliding flight	31 (2,58 %)	2 (7,14 %)
12. Ascending flapping flight - "Retracted head" Flapping flight	21 (1,75 %)	
13. "Horizontal" flapping flight - "Retracted head" Gliding flight with a turn	16 (1,33 %)	
14. "Horizontal" flapping flight- "Retracted head" Gliding flight	16 (1,33 %)	
15. Gliding flight - "Retracted head" Gliding flight with a turn	15 (1,25 %)	
16. Gliding flight - "Retracted head" Flapping flight	15 (1,25 %)	1 (3,57 %)
17. Ascending flapping flight - "Retracted head" Gliding flight with a turn	11 (0,92 %)	
18. Ascending flapping flight - "Retracted head" Gliding flight	4 (0,33 %)	
Total	**1200**	**28**

Table 17.
Comparison of flights, paths and postures distribution between both species

		COMMON SWIFT	ALPINE SWIFT
Captures number		**1200**	**28**
Flight before capture	Flapping	81 %	29 %
	Gliding	19 %	71 %
Head posture	"Projected"	78 %	64 %
	"Retracted"	22 %	36 %
Flight after capture	Flapping	50 %	21 %
	Gliding	50 %	79 %

9.C.1. Captures after an ascending flapping flight

On 16 August 2018, in 3 out of 28 videos, the Alpine Swift made a capture after an ascending flapping flight (**Table 18**).
Common features with Common Swift:

- bell-shaped ascending path;
- flapping flight with rectrices spread out.

Different features with Common Swift:

- a slightly longer average duration (1.02 s) than in Common Swift (0.78 s);
- a slightly lower average wingbeat frequency (8.2 Hz) than in Common Swift (9.4 Hz).

One more time, these differences can be correlated with the sizes differences between both species.

Table 18.
Three captures preceded by an ascending flapping flight in the Alpine Swift
Vidéo

VIDEOS	Hunting flight	Ascending flapping	Capture	Flight after capture
P1100049	Flapping flight Fréquency: 6,5 Hz	Duration: 0,833 s Fréquency: 8,4 Hz		Gliding flight
P1100165	Gliding flight	Duration: 0,719 s Fréquency: 8,3 Hz		Flapping flight Fréquency: 5,7 Hz
P1100175	Gliding flight	Duration: 1,511 s Fréquency: 7,9 Hz		Gliding flight

9.C.2. Prey detection

As in the Common Swift, the beginning of the ascending flapping flight can be considered as the moment when the Alpine Swift has visually detected a prey item. In the 3 previous examples (**Table 18**), the duration of the ascending flapping flight is calculated but without information on speed, it is not possible to deduce the distance travelled.

Unlike the Common Swift, it seems to me that the Alpine Swifts show more signs of a change in behavior that can be interpreted as when the prey is detected: tilting of the body, steady gaze in the supposed prey direction...

Both species of swifts have similar head morphology and anatomy (**Figures 29 and 30**). The low mobility of the eyes is compensated by very rapid head movements (**Figures 31 and 32**).

Figure 29.
Common swift

Figure 30.
Alpine Swift

Figure 31.
Head mobility of the Common Swift

Figure 32.
Head mobility of the Alpine Swift

9.C.3. Head postures

The two postures, head "retracted" and head "projected" can be observed in Alpine Swifts. In both species, head forward projection in the direction of flight is the most common (**Table 19**).
It is often associated with the body projection with the lowered wings, spreading tail in a fan shape and neck stretched upwards (**Figure 33**).
The absence of head projection sideways is certainly related to the low number of data.
The 3 captures with a head downward projection could be a feature of the Alpine Swift, as the Common Swift only rarely shows this type of projection (0.8 %). However, additional data are needed to establish a possible difference.

9.C.4. Beak and mouth cavity

Like the Common Swift, the Alpine Swift has a small blackish triangular beak that can open wide under the eye to reveal a large gap.
Beak opening amplitude is also variable and is not directly related to prey size since a maximum amplitude can be observed for very small, non-visible prey (thumbnails in **Table 18**).

9.C.5. Eyelids

Common Swifts and Alpine Swifts have large eyelids to protect their eyes. When capturing while opening their beaks, very frequently the eyelids close partially or completely (**Figure 34**).

Table 19.
Distribution of the 4 directions of the head's "projection" in both species

	COMMON SWIFT	ALPINE SWIFT
Head forward projection	409 (43,5 %)	9 (50 %)
Head upward projection	278 (29,6 %)	6 (33 %)
Head sideward projection	245 (26,1 %)	0
Head downpward projection	7 (0,8 %)	3 (17%)
Captures with projection	**939**	**18**

Figure 33.
Capture with body upward projection

Figure 34.
Capture with half-closed eyelids

9.C.6. Capture in inverted flight

Like Common Swifts, Alpine Swifts are able to switch to inverted flight (**Figure 35**) by rotating the wings, while the head remains fixed. In this example, the rotation is faster than in the case of the Common Swift (**Figure 9**).

Similarly, Alpine Swifts are able to capture prey in inverted flight (**Figure 36**). This ensures better positioning and effective slowing before capture.
For the moment I have no documents on a possible social function of inverted flight in the Alpine Swift.

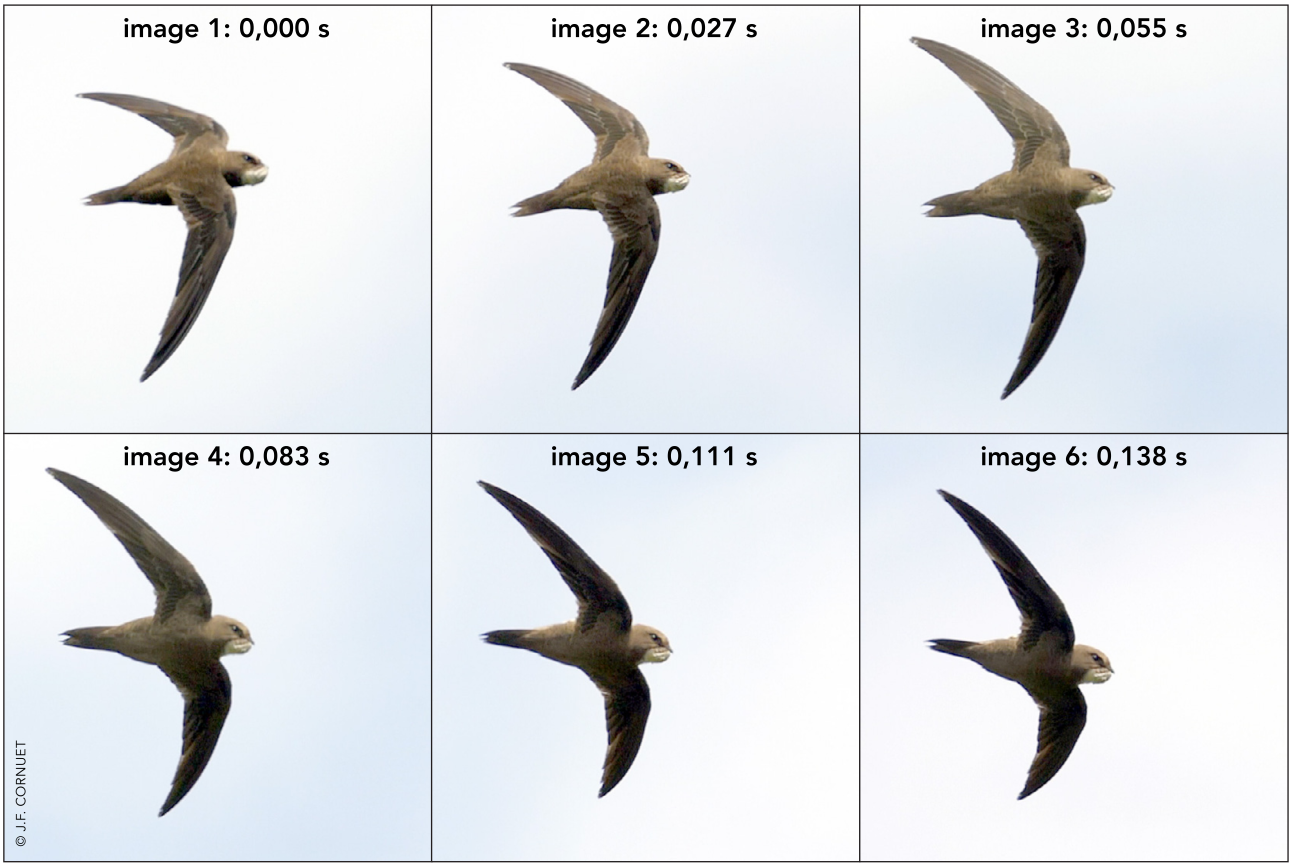


Figure 35.
Body rotation of the Alpine Swift during the passage in inverted flight. The head remains fixed.

Vidéo

Figure 36.
Alpine Swift, prey capture by an inverted flight

Vidéo

9.D. Beak opening and closing

Like Common Swifts, Alpine Swifts forage with their beak closed. They open it only for a very brief moment upon capture.

Compared with the Common Swift, the average duration of beak opening and closing is very similar (**Table 20**). In both species, the beak opening-closing cycle does not exceed one-tenth of a second (maximum 0.0944 s in Alpine Swifts). The upper thousandths of a second values in Alpine Swift are again correlated with its upper dimensions (**Table 15**).

It would be interesting to see if the average prey size, which is generally higher in Alpine Swift, has an impact on the average length of the beak opening-closing cycle.

Table 20.
Average beak opening and closing durations in both species

		COMMON SWIFT	ALPINE SWIFT
Captures number		1200	28
Beak opening	Minimum value	0,0111 s	0,0111 s
	Average duration	**0,0214 s**	**0,0272 s**
	Maximum value	0,0666 s	0,0777 s
Beak closing	Minimum value	0,0055 s	0,0083 s
	Average duration	**0,0113 s**	**0,0153 s**
	Maximum value	0,0277 s	0,0277 s
Opening + Closing	Minimum value	0,0166 s	0,0222 s
	Average duration	**0,0327 s**	**0,0425 s**
	Maximum value	0,0833 s	0,0944 s

Alpine Swift getting ready to catch a prey item

9.E. Captures with visible prey

9.E.1. Calculations

As with the Common Swifts, some videos of the Alpine Swift show prey that can be followed until capture. They provide information that allows the same calculations to be made as for the Common Swift.

For the latter, out of the 52 videos studied, 2 results were obtained on the breeding-station:

- the average speed of Common Swifts is 7.9 m/s;
- the distance from the prey to the beak when the beak begins to open is 17 cm.
-

In the Alpine Swift, it is difficult to average with only 5 captures (**Table 21**). However, several remarks can be made.

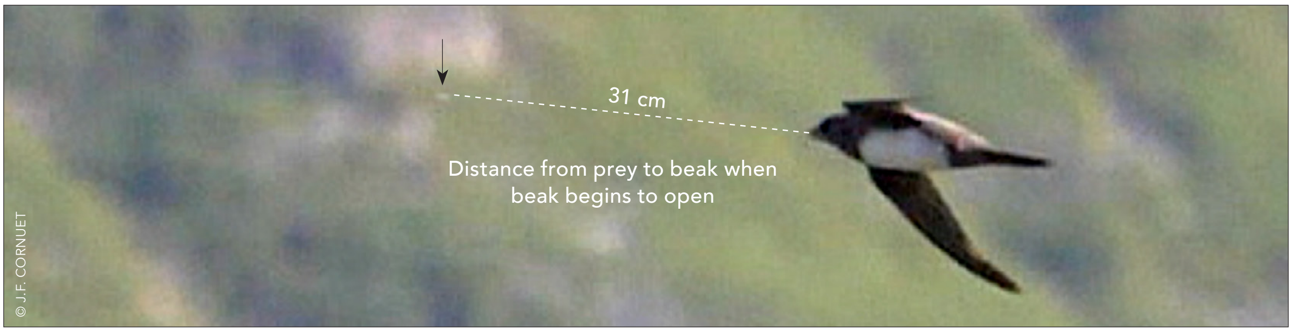
First of all, the Alpine Swift's speed at capture time shows extreme values that vary from single to triple (minimum value of 6.2 m/s; maximum value of 19.7 m/s). These speeds are mostly higher than the average speed calculated for Common Swifts (7.9 m/s). The hunting flight of the Alpine Swift, under the conditions studied, is therefore faster than that of the Common Swift in the breeding-station.

The lowest speed (6.2 m/s) is easily explained: it is measured on a capture made in inverted flight (**Figure 36**), one of the functions of which is to brake the bird to make the capture easier.

Like speed, the distance from the prey to the beak when the beak begins to open has extreme values ranging from single to quadruple (minimum distance of 11 cm; maximum distance of 44 cm). **As with Common Swifts, these values confirm that the Alpine Swift opens its beak at the very last moment before capture, which is consistent with the short opening-closing cycle of the beak (0.04 s) and shows the very efficient neuro-muscular capacities common to both species.**

Table 21.
Data from 5 captures by the Alpine Swift where the prey is visible

VIDEOS	Maximum distance the prey becomes visible	Swift speed over this distance	Distance from prey to beak when beak begins to open
P1100145	0,656 m	19,7 m/s	26 cm
P1100147	1,482 m	13,0 m/s	31 cm
P1100160	2,539 m	16,3 m/s	44 cm
P1222605	1,610 m	8,9 m/s	22 cm
P1222607	1,019 m	6,2 m/s	11 cm



9.E.2. A multi-step capture

A capture with visible prey is interesting to detail because it is made in several steps over a period of nearly 4 seconds (**Figure 37**).

Step 1
The bird is gliding. Suddenly it rises in an energetic ascending flapping flight: a prey has been spotted but it is not in the filmed field for the moment.

Step 2
The bird stops flapping its wings, glides with its wings extended and its tail fanned out while following the progress of the prey as it enters the field (it is not visible on the thumbnail).

Step 3
The prey flies in front of it without the bird projecting towards it.

- Is the capture failure due to the bird's misjudging of the prey's path and distance ?
- Is it a giving up after detection of potentially at-risk prey?

Step 4
The prey quickly disappears from the filmed field, but suddenly the bird turns sharply on the wing and dives in a flapping flights as if it were chasing the prey.

Step 5
Following the bird's path the prey appears again in the field and this time the bird succeeds in capturing it.

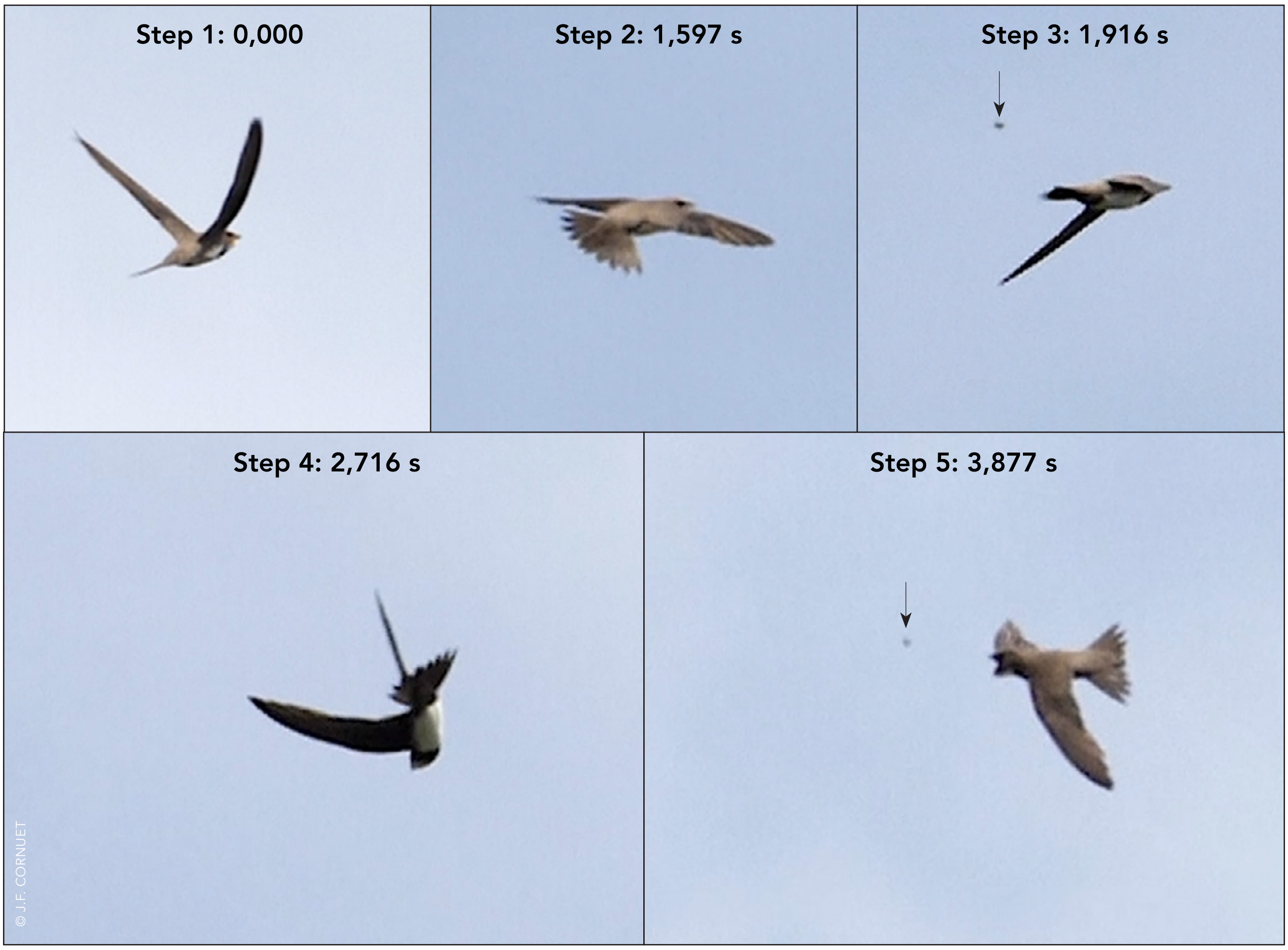


Figure 37.
Alpine Swift: a capture in five steps

Vidéo

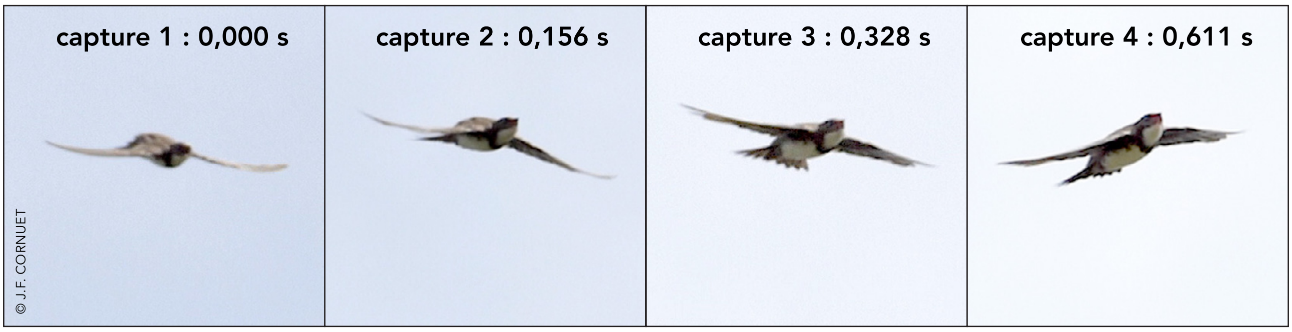


Figure 38.
A sequence of 4 captures in only 0.62 seconds.
Vidéo

9.F. Time intervals between 2 consecutive captures

Among the 28 videos of the Alpine Swift, one is notable for a sequence of 4 captures in only 0.611 s, i.e. an average interval between each capture of 0.204 s (**Figure 38**). It is possible that these captures were made in a swarm of insects because columns of insects were visible on the site (flying ants...).

The video shows that the bird chains the 4 captures during a gliding flight marked at each capture by:
- a slight lowering of both wings;
- an head upwards straightening;
- an beak opening and closing.

In the Common Swift, we had seen that a bird with a bolus could chain 3 captures in 0.532 s with equal intervals of 0.266 s between each capture (**Figure 22**).

9.G. Captures with bolus

Like Common Swift, Alpine Swift feeds their chicks with balls of prey stuck together with saliva (bolus). Of the 28 captures, 8 are made by adults with a bolus. As in the Common Swift, the transport of the food ball into the gap does not seem to have a significant impact on the capture skills of the Alpine Swift. Only a very slight increase in the beak opening-closing cycle can be noticed in both species. However, the presence of a bolus does not prevent the bird from projecting itself towards prey (**Figure 39**).

9.H. Comparison results

The comparison with the Alpine Swift foraging confirms the behavioral proximity of the two species, already noticed in the grooming study.
The small quantitative differences are mainly due to the larger size of the Alpine Swift.
.

Figure 39.
Alpine Swift adult with bolus capturing prey

10. Outstanding issues

This captures study therefore made it possible to describe the different types of flights and postures used in the feeding behavior of the Common Swift.
However, many questions remain unanswered for the moment. Here are two examples.

10.A. Are the foraging behaviors of the Common Swift innate?

A young swift when it leaves the nest is not taken care of by the adults as is the case, for example, with the swallows of our regions [Barn Swallow (*Hirundo rustica*), Eurasian Crag Martin (*Ptyonoprogne rupestris*) ...] which remain for some time in family groups where youngs live alongside adults and can learn foraging by imitation while continuing to be fed. In this way, in-flight feeding, which is frequent in these species, helps to develop motor skills useful for the independent foraging flight of the young.

The young swift does not benefit from this assistance from the first days. Rather, it flies away at dusk in the evening and quickly leaves the colony (Genton, 2016)), where it does not return.

If this first flight takes place during the day, it is then possible to see some innate behaviors. For example, a young bird just out of the nest has been observed grooming itself 3 to 4 times by contortion with rubbing..., another has shown typical prey capture behavior (B. GENTON, personal communication, 12 August 2019).

It is therefore highly likely that the basic foraging and grooming behaviors of Common Swifts are innate with a progressive improvement in efficiency through mimicry in the learning phase following the first flight (G. GORY, personal communication, 12 August 2019).

In a natural environment close to large rivers, some young-of-the-year can be observed outside the colony: for example, behaviors (drinking, foraging, grooming...) can be observed. However, the difficulty remains to know for sure whether one is in the presence of young-of-the-year or older individuals (G. GORY, personal communication, 9 July 2019).

The young-of-the-year swifts are visually distinguished by:

- **their large white chin;**
- **their white forehead;**
- **their overall lighter hue;**

the pale edges of the wing and tail feathers (Figure 40).
(B. GENTON, personal communication, 12 August 2019).

With the help of binoculars, an observer, who is very familiar with swifts, could be able to distinguish between youngs-of-the-year flying in the middle of a flock of individuals of different age groups.

On the other hand, the shorter wing feathers length criterion of 5% in the young-of-the-year cannot be observed in the wild.

The scarcity of young-of-the-year observations in the wild explains why, to date, despite extensive research in the media (books, magazines, internet...), I have never seen photographs of a young-of-the-year in flight.

Figure 40.
Portrait of a young Common Swift in profile

10.B. What are the sensory skills of the Common Swift?

This is a very broad problem that goes beyond the scope of this paper. I would limit myself to two specific questions.

10.B.1. How far can Common Swift detect a prey item from?

The question arose on page 154: the triggering of the ascending flapping flight appears to be related to the detection of prey. The average duration of this flight is 0.780 seconds. If we could measure the speed, we could know the distance travelled and therefore the detection distance. Obviously, this distance depends on the size of the prey. With the detection distance and the size of the prey, the visual acuity of the bird could be evaluated.

But what do we know about the eye and visual skills of Common Swift?

Common Swift eyes are well protected by an eyebrow arch made up of small, stiff feathers (**Figure 40**).

Retina histology has been studied: it has only a lateral fovea and contains more cones than rods (Oehme, 1962).

Cones promote daytime colours vision and their high density, particularly at the fovea, is an essential condition for visual acuity.

Rods are useful for night vision. With a lower density of rods, Common Swifts see better in daylight than at dusk or in the dark.

Based on Oehme's work, Brückner (Brückner, 1990) made numerous ophthalmological measurements on live swifts, both young and adult.
The few elements below are taken from his very comprehensive article.

Swift eyes have internal protection against strong sunlight.
Accommodation (focusing on the retina) is done more by the curve of the cornea than by the deformation of the lens.
Common Swifts have a binocular field of vision of 24° forward...

Brückner thinks that the Common Swift has a true vision of relief (stereopsis).

The Common Swift, like the other birds, compensate for the low mobility of the eyes by jerky head movements (**Figure 41**).

Based on all his ophthalmological observations and measurements, Brückner presents a theory on the visual detection of prey in Common Swifts.

10.B.2. How does Common Swift detect the dangerousness or harmlessness of a prey?

The question had arisen in the study of prey selection examples (pages 167 to 170).
How does swift distinguish between a worker bee with a sting and a male drone without one?
How does swift recognize a harmless hoverfly with the appearance of a small wasp?

Hypothesis 1: Recognition would be visual. Birds perceive part of the UV spectrum on the retina.
Perhaps the worker bee and the drone on the one hand, the hoverfly and the wasp on the other hand reflect UV differently? (Dalton, 2005).

Hypothesis 2: Recognition would be auditory. Swift could perceive differences in the sounds emitted by the flight of these insects.

Hypothesis 3: Recognition would be both visual and auditory.

Figure 41.
Common Swift flying frontview and turning head to its right

Conclusion

At the end of this paper, it appears that further studies on the foraging of the Common Swift should be conducted in other environmental contexts in order to establish possible variations according to weather conditions, size and density of available prey, time of year, etc...
The sensory world of this bird also remains to be explored.
Similarly, a more in-depth study of the Alpine Swift foraging skills on different sites is essential to refine its trophic behaviors.
It would also be very interesting to look into the case of the Pallid Swift (*Apus pallidus*), the third species of swift breeding in France. Does it hunt like the Common Swift or does it have its own specific behaviors?

From a methodological point of view, rotational stereo-videography and slow-motion video monitoring techniques should be used together to study the flight behavior of many bird species.
The gear that could make the synthesis between the two techniques is to be invented.

One can dream of a pair of stabilized binoculars with:

- a measuring system similar to the one used in police radar binoculars to record the physical parameters of the flight and reconstruct its 3D trajectory;
- and a slow-motion video recording system to describe the bird's behaviors in detail.

After grooming and foraging, a next paper could deal with other aerial behaviors and more particularly social behaviors: dihedral flying, screaming parties...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Screaming party at dusk

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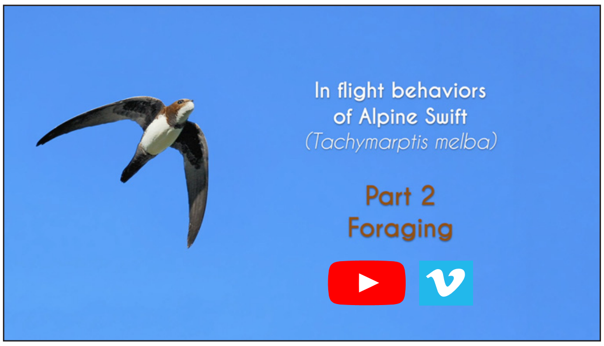
Vidéos



Acknowledgements

Thanks to Ulrich TIGGES for his most relevant comments, constant availability and for providing his literature resources.
Thanks to Bernard GENTON for sharing his observations and for his careful proofreadings.
Thanks to Gérard GORY for sharing his observations and for his most relevant comments.
Thanks to Peter CUSH for our very rich exchanges and for improving this English version of this paper.
Thanks to Emmanuel de MARGERIE for his help and advice for data processing.
Thanks to Michel BARATAUD for his availability and for his careful proofreadings.
Thanks to my friends Jean-François DESMET and Jacques BLONDEL for their support and encouragement.
Thanks to Valérie, my wife, for her careful proofreadings.

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ISSN 2607-0510