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

Part 1 Grooming

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Abstract

In May, June and July 2017 and 2018, 65 days were devoted to video recording the behavior of Common Swifts (Apus apus) flying over a small urban colony in the suburbs of Paris (France). The first aim of this work was to capture through video recording various flight behaviors. The first tests showed that only flight tracking with slow motion shooting could provide valuable video data. The choice of equipment was based on the Panasonic GH5 hybrid camera, which had just been launched on the market in April 2017. This camera allows shooting in HD at a frame rate of 180 fps, or 6 times slower.(17%). With its ergonomics and electronic viewfinder for easy manual focusing (Focus Peaking), this device is well suited for freehand tracking of the very fast flight of swifts. Nearly 1400 videos were captured with the GH5 and a Nikkor 4/300 AFS telephoto.

55 Plume de Naturalistes n°3 - 2019 The different kinds of flights (flapping, gliding, inverted,...) and social behaviors (dihedral flight, duo flight,...) amounted to 64 % of videos.

Preys catches in flight represented 25 % of videos, and, 11 % of the videos present various in-flight grooming behaviors. The latter has been analyzed in Part I.

Settled down in the nest, breeding adults and immature explorers spent part of their time maintaining their plumage during individual or mutual grooming sessions between the two partners.

Outside the breeding season, swifts spent all the time on the wing. They hadtherefore to develop particular in-flight grooming behaviors.

With their neck extension facility and general flexibility of the body, swifts use their beak to groom both the chest and the back. By bending backwards strongly, the bird is able to reach the uropygial gland, including preening the tail feathers. Although quite short, legs are mainly used to vigorously scratch head and neck. Like all species that can head scratching in flight, the Common Swift succeeds to pass the leg under the wing to reach the head.

In addition to these classic grooming behaviors, swifts combine various kinds of in-flight acrobatic figures that can be accurately described with slow motion video. The bird shakes its whole body, rubs its wings together, twists its head very quickly with beak open or closed.

These videos show that the Common Swift is fully able to perform complete body maintenance in flight. To limit altitude loss during these in-flight grooming operations, the bird has developed 3 complementary strategies:

• it anticipates the loss of altitude by a short preliminary ascent flight,

- it reduces altitude loss by increasing lift through gliding,
- it reduces altitude loss by very short grooming times equal to or less than one second.

The speedness of these behaviors is presumably one of the main reasons why these behaviors have so far been little studied in detail. Only a sufficient slow motion video at close range is able to provide a precise description of these behaviors.

Finally, it is clear from the videos that swift seeks to maintain a good perception of its environment at any time by maintaining the inclination of the frontal plane at or near 0° to the horizon using coordinated movements of the wings, legs and tail.

Based on this analysis, a first behavioral catalogue of in-flight grooming is proposed for the Common Swift.

The extension of this study to other bird species reveals characteristics common to groups practising in-flight grooming :

- rather long and tapered wings reflecting excellent aerial skills and an ability to spend most of their lives in the sky for foraging and travelling over long distances,...
- the two most frequent grooming behaviors are : head and neck scratching and underside grooming with the beak.

Introduction

For nearly a century, Common Swifts (Apus apus) have been and continue to be the subject of a huge number of observations and studies. Ulrich Tigges, Webmaster of www.commonswift.org, identified until 2016 nearly 6 000 publications on this species. All aspects of the biology and behavior of this bird have been explored within the limits of field techniques. Many laboratory studies have also been conducted on the amazing aerodynamic capacities of this bird. We know that the Common Swift spends most of its life on the wing for moving, migrating, feeding, grooming, sleeping, finding nest material, and eventually mating...

IWhen sitting in the nest under the roof of a house, aspects of the behavior of the swift are well known because their observations do not involve any real technical problems. In contrast, its aerial behavior is much more difficult to record and describe in detail. The bird's small size (42 to 48 cm in wingspan), its fast flight (10 m/s on average) and the brevity of its behavioral items are the main problems to be solved to access this knowledge. Fortunately, near breeding sites, individuals can be observed in flight at a short distance for hours.

Visual observation made it possible to describe the two main types of flight, flapping and gliding. But observing and interpreting some very rapid behavioral items lasting less than or equal to one second is quite challenging.. In the late 1960s, some authors (e.g. OEHME, 1968 ; ROTHGÄNGER, 1973) started using a film camera to try to capture what the observer could not see. These pioneers were the first to describe very brief behaviors such as inverted flight or postures associated with plumage care. To my knowledge, they were not followed by others in this direction. I first started to take pictures of birds in flight, using moving pictures (1979). Then I used more intensively digital device from 2007 to 2012. Of the thousands of photos I took at that time, the vast majority only show flight postures with no particular behavior. Sometimes I got some spectacular images such as prey catches, or a grooming image where the bird scratches its head with its claws , as well as, postures much more difficult to interpret.

In 2017, the release of the Panasonic Lumix GH5 hybrid camera gave me the opportunity to shoot in FHD (1080p) at a maximum frame rate of 180 fps.

The reading at 30 fps of the rushes shot in 180 fps made me discovering for the first time in slow motion the details of very brief behavioral sequences. The videos have been classified into 3 categories (**Table 1**).

Distribution of videos shots in 2017 and 2018			
	2017	2018	2017 + 2018
IN-FLIGHT CAPTURES	179	169	348 (25 %)
IN-FLIGHT GROOMING	73	80	153 (11 %)
ONLY FLIGHTS	267	622	889 (64 %)
Totals	519	871	1390

Table 1. Distribution of videos shots in 2017 and 201



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 65 days : 33 in 2017 (from 25 May to 16 July), and 32 in 2018 (26 May to 19 July) between 6:00 am and 11:00 am (four hours on average).

A few pairs of Common Swifts also 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 decade of May with the gradual arrival of 1st, 2nd and 3rd year immatures. As nonbreeding 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 from July 20.

Shooting gear

I used the Panasonic Lumix GH5 with the Nikkor 4/300 AFS lens. 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
- 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.

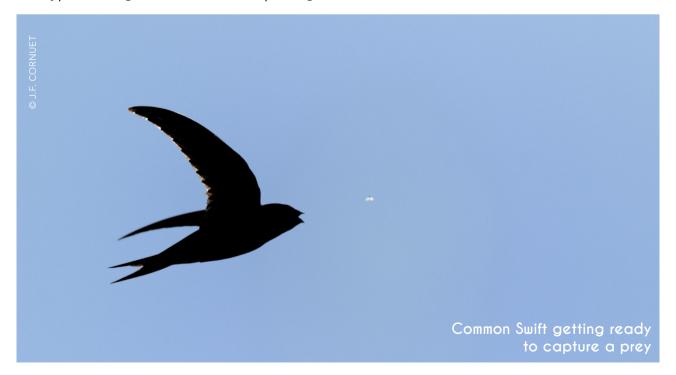
Is the variable rate of 180 fps enough for properly filming a Swift in flight ?

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 the 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 picture below of a swift in flight with its beak open with an insect flying a few centimeters in front of it.

This is an uncommon but not exceptional document since such images can be found on the Web. Having taken several thousand photographs of foraging swifts, I succeeded to capture but a few sharp images of such an action. With a good shooting rate (12 fps) camera I have saw nor obtained a sequence of images showing what happens just before and just after the shot. However, this type of image can lead misinterpreting the hunting mode of the Swift. Indeed, I was very surprised to read on pages of reputable ornithological Websites that Swifts were hunting by stealing with their beaks open! This is a false and surprising statement in 2018, knowing the problem had been solved since decades by eminent ornithologists (LACK, 1956, GÉROUDET, 1980. MAYAUD 1936...). From the hundreds of shots I succeeded to film 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 a second. The slow motion video therefore provides formal proof that the 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 moving 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 photo of 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 the swift. Moreover, the autofocus is automatically disabled on GH5 when it is set to variable frame rate.

For good manual focusing, one needs 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

On original videos not slowed down in post-production, the duration of behavioral items and wing flapping frequencies were calculated based on the image duration (1/180s). For example, a behavior that occurs over 240 images lasts 240/180 = 1.33 s. 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.

Video analysis

Each type of grooming is described using examples presented in the form of a sheet of thumbnails from a video. The time intervals between each image are specified to the thousandth of a second. If necessary, the behavior is further analyzed.

Grooming average time and frequency are calculated. A discussion was initiated based on the data found in the literature.



Comparison with other species

The study of behavioral traits of Common Swifts in flight led me compare them with those of other species.

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

While searching in my pictures and videos library, I found several scenes of in-flight grooming in different species of swallows, raptors,...

I finally extended the search to images found on the Web for which I mentioned direct link.





Introduction to in-flight grooming

During the two study periods (May 25 -July 16, 2017; and May 26 - July, 2018), breeding adults spend a large part of their time at the nest for maintaining their plumage during individual or mutual preening sessions between the two partners.

On the other hand, immature individuals and non-breeders have little or no opportunity to land during their first years of life. These individuals take care of themselves while flying, unless they land, alone or in pairs, for prospecting future breeding sites.

Common swifts face at least two body issues:

- Like any bird, they have to keep their plumage in good order, removing dust and dirt and rearranging the beards and barbules of the feathers,...
- Like many birds, they hosts parasites that cling on feathers or skin, the most famous and species-specific of which is

Table 2.

Crataerina pallida, a haematophagous insect (Diptera, Hippoboscidae). This ectoparasite feeds on blood from the chick stage onwards and is quite common in the Common Swift.

Common Swift uses water for bathing. Wetting his plumage may arise from:

- striking the belly in flight on the surface of a lake or pond;
- enjoying rain, although Swifts don't seem to like it very much.

These kinds of behavior were not observed in this study, but are well known (BERSOT, 1931) and **documented**.

In flight, the Common Swift cares for its plumage in different ways:

- From reaching the back, tail, chest and belly with the beak;
- From head-scratching with the legs;
- Making contortions, accompanied by fluttering and rubbing of the wings on the body. (**Table 2**).

		2017	2018	2017 -	- 2018
	Back and upper coverts	24	33	57	37.25 %
	Tail feathers	2	1	3	1.96%
Preening with beak	Chest and belly	10	11	21	13.72 %
	Legs	1	0	1	0.65 %
Grooming with the legs claws - Head-scratching		10	10	20	13.07 %
	Contorting and rubbing	17	17	34	22.22 %
Grooming with whole-body move-	Wings fluttering	3	2	5	3.27 %
ments	Rolls	1	1	2	1.31 %
Grooming by head	Head rotation with closed beak	3	2	5	3.27 %
rotation	Head rotation with open beak	2	3	5	3.27 %
	TOTALS	73	80	153	100 %

Different grooming behaviors studied in the Common Swift



1. Grooming with the beak

In birds, in addition to its role for foraging, the beak can be used to clean, rearrange feather beards and barbules, get rid of parasites provided they are not too firmly attached to the body such as like mites. The use of the beak while grooming is visible in 82 videos.

1.1. Preening back and upper coverts of wings with the beak

57 videos show grooming feathers on the back and for some upper covers of the wing.

The **Figure 1** shows the bird partly in profile.

Captions in Figure 1

- **thumbnail 1**: the swift is in flapping flight, with semi-open tail feathers ;
- **thumbnail 2**: it stabilizes in gliding flight, with wings and tail spread widely for maximum lift;
- **thumbnail 3**: the bird stretches its neck, turns head 180° and grooms the feathers on upper back and wing base covers with the beak. Eyelids are closed.
- **thumbnail 4**: in this side view, the bird appears headless, keeping its wings curved backwards;
- **thumbnail 5**: the head returns to its previous position;
- **thumbnail 6**: the bird keeps on gliding.

Video

thumbnail 1 : 0.000 s	thumbnail 2 : 0.238 s	thumbnail 3 : 0.344 s
thumbnail 4 : 0.566 s	thumbnail 5 : 0.972 s	thumbnail 6 : 1.077 s

Figure 1. Preening back and upper coverts of wings with the beak





Freehing back and opper coverts of wings with the be

The **Figure 2** shows a bottom view with the typical «headless bird» posture as in thumbnail 4.

Captions in Figure 2

- **thumbnail 1**: the swift rises in flapping flight;
- **thumbnail 2**: it stabilizes in gliding flight, with wings and tail spread widely for maximum lift;
- **thumbnail 3**: the bird begins to rotating its head;
- thumbnail 4: the bird is preening the feathers on the upper back. In this bottom view, it looks headless, trying to maintain balance with its asymmetric wings;
- **thumbnail 5**: the head returns to its previous position;
- **thumbnail 6**: the bird keeps on gliding.

Grooming average time

When looking at more precise limits of the behavior on 57 video shots, the beginning and end of head rotation to the back, grooming average duration is 1.00 s.

Behavior frequency

Of the 153 grooming behavior items recorded in flight, 57 concern this one, i.e. 37.25% of the total (Table 2).

In 2018, 3 different shots show that a single bird can achieve a sequence of 2, 3 and up to 6 back grooming operations. These sequences must even be more frequent than suggested by these 3 data because of the difficulty of following an individual for a certain amount of time. In the 6 back grooming shots, the action lasts 14 seconds and ends with a grooming by contorting and rubbing.



Trajectory study

The comparative analysis of the 57 shots shows a sequence of actions along a bell-shaped path (PICHOT, 2017) (**Figure 3**):

- After a flapping flight to rise (which is not always the case), the bird begins to glide, with its wings wide apart and tail fanned out to increase the body surface area and therefore lift to limit altitude loss. Sometimes in this preparatory gliding flight the bird stands with its head up.
- The bird turns its head 180° backwards: seen from below, it seems having lost its head.
- With the beak, the bird is preening the plumage of its back and wing base (lesser and median coverts).
- The wings can:
 either be well spread to maintain

the inclination of the frontal plane equal to or close to 0° with respect to the horizon and slow down the descent;

 or move backwards by lifting or lowering at the same time as the bird's back more or less curves

Discussion

In **1961**. D. I. M. WALLACE is apparently the first author to have mentioned this behavior of the Common Swift in a note published in *British Birds*.

The note is illustrated with a sketch. (Figure 4).

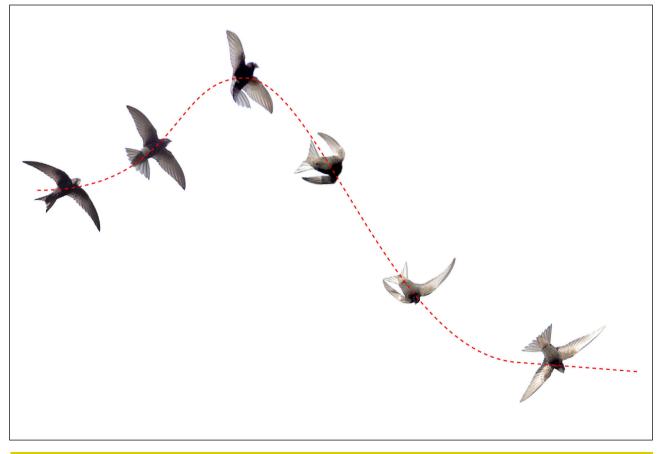
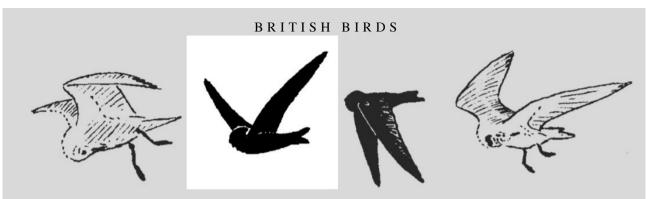


Figure 3. Bell-shaped path during back preening (according to PICHOT, 2017)





Some attitudes adopted by (*left to right*) Black-headed Gull (*Larus ridibundus*), Swifts (*Apus apus*) with wings elevated and depressed, and White-winged Black Tern (*Chlidonias leucopterus*) when preening in the air (see text) (*sketches D. I. M. Wallace*)

Figure 4.

First mention in the literature of in flight back grooming behavior in the Common Swif (WALLACE, D.I.M., 1961)

The two central birds are Common Swifts. The first with elevated wings is preening its upper back, while the second with depressed wings is preening its chest.

In **1973**, G. ROTHGÄNGER & H. ROTHGÄNGER, described a head twisting for grooming.

Der Kopf ist bei diesem Verhalten zur Brust, zum Rücken oder zu einem Flügel gewendet. Dabei werden stoßartige Bewegungen ausgeführt. Die Flugbahn verläuft allmählich ansteigend, bis die Geschwindigkeit derart vermindert ist, daß ein Abflug erfolgt. Die beschriebene Handlung kann sich einige Male wiederholen... Wir sehen in dieser Flugweise eine Säuberungshandlung, bei der zwischen einer aktiven (Anstieg der Flugbahn) und einer passiven Phase (Abflug) unterschieden werden kann.

A quotation that can be translated as:

The head is turned to the breast, to the back or to a wing. Thereby, shock-like movements are performed. The trajectory gradually increases until the speed is reduced in such a way that a descent takes place. The described action can be repeated several times.... This type of flight is interpreted as a grooming action can be distinguished between an active phase (elevation) and a passive phase (beginning of grooming).

In **1998**, Yves Garino, described a similar behavior that he described as «vol décroché - stalled flight» On some days, Swifts glide normally, then stall (they loss speed) voluntarily several times in a row. At the same time, they seem to preen the leading edge (front edge) of a wing with their beak.... Sometimes several birds behave similarly and simultaneously, although they are far apart from each other.

The last sentence suggests socially contagious behavior, which I could not observe because of my tight framing on the birds.

In **2017**, CÉCILE PICHOT in her research paper clarifies the function of bell-type flying, which was already described by ROTHGÄNGER in 1973.

On distingue une phase active (élévation) et une phase passive (début du toilettage)... La position en flèche qui est alors adoptée pourrait s'expliquer par le fait que l'oiseau doive se contorsionner pour atteindre les diverses parties de son corps. Cette position entraînant une perte d'altitude, on peut imaginer que la trajectoire en cloche va permettre de diminuer cette perte d'altitude en en provisionnant un peu dans un premier temps (cf. partie ascendante de la cloche).

A quotation that can be translated as: A distinction is made between an active phase



(elevation) and a passive phase (beginning of grooming).... ... The arrow position that is then adopted could be explained by the fact that the bird must twist itself to reach the various parts of its body. As this position leads to a loss of altitude, it is conceivable that the bellshaped trajectory will make it possible to reduce this loss of altitude by making some provision for it at first (see the rising part of the bell).

Comparaison with Alpine Swift

I filmed 5 in-flight back grooming behaviors in Alpine Swift.

The same postures and movements as those described in the Common Swift have been

recorded (Figure 5).

However, the average duration of this grooming has been 75% longer (1.75 s compared to 1.00 s in the Common Swift) which can be explained by larger dimensions of the Alpine Swift (25%) than those of the Common Swift (**Table 3**) ensuring better lift when the bird stops flapping its wings to groom its back.

Some examples of pictures accessed on the Web on 01/12/2018. (Figure 6)

Table 3.

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



Figure 5.

Three pictures from videos of Alpine Swift grooming its back in flight. The classic «headless» posture observed in the Common Swift can be recognized

3











Video

Figure 6.

Five examples of pictures of birds grooming their backs 1 : Common Swift ; 2 : Common Swift ; 3 : Little Swift (*Apus affinis*) ; 4 : Black-legged kittiwake (*Rissa tridactyla*) ; 5 : American white ibis (*Eudocimus albus*).

To watch these pictures on the Web, click on thumbnails (Accessed on 25/11/2018)



1.2. Preening tail feathers with the beak

Three shots show that the bird is able to reach the tail feathers in flight to preen them. As with back grooming, the bird turns its head by 180°. By digging its back and lifting the tail feathers, he manages to grasp the feathers in its beak one by one for preening them.

Captions in Figure 7:

- **thumbnail 1**: the swift is gliding;
- thumbnail 2: the bird turns its head;
- thumbnail 3: the bird curves strongly and straightens its tail vertically. It preens a first tail feather;
- thumbnail 4: the bird preens a second tail feather;
- thumbnail 5: the bird stops preening, turns its head and reduces its curvature:
- thumbnail 6 : the bird keeps on gliding.

Grooming average time

In the 2 shots of 2017, the bird preens each time 3 tail feathers in 1.33 s.

In the 2018 single shot, the preening of a tail feather is visible on 30 images or 0.166 s.

Behavior frequency

Among 153 grooming behavioral items recorded in flight, the three concerning preening the tail feathers amounted to 1.96% of the total (Table 2).

Discussion

I found no specific mention or picture in the literature of the observation of this behavior. The video in Figure 7 shows that the bird while bending reaches the uropygial gland near the rump. He extracts the secretion with the beak before preening the tail feathers

thumbnail 1 : 0.000 s	thumbnail 2 : 0.066 s	thumbnail 3 : 0.416 s
	*	
thumbnail 4 : 0.811 s	thumbnail 5 : 1.222 s	thumbnail 6 : 1.338 s
		N/t 1

Figure 7. Preening tail feathers with the beak

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Video

1.3. Preening chest, belly and lower coverts of wings with the beak

The process of grooming the feathers of the chest, belly and probably the lower covers of the wing base is visible in 21 videos.

Captions in Figure 8 :

- **thumbnail 1**: the swift is gliding, but the tail feathers are not spread;
- **thumbnail 2**: with the eyelids closed*, the bird begins tilting its head down;
- **thumbnail 3**: the bird begins preening the chest feathers with its beak;
- **thumbnail 4**: the bird continues preening the chest feathers with its beak;
- **thumbnail 5**: the head returns back to its previous position;
- thumbnail 6: the bird keeps on gliding.

*Eyelids closed : DEREK BROMHALL in 1980. in his book Devil Bird, The Life of the Swift, page 52 wrote about nest grooming: « The birds always closed their eyes when preening. »

Of the 21 shots showing the chest and belly grooming, the shot described in the **Figure 8** is the only one where the tail is closed throughout the behavior, while in the other 20 shots tail feathers are well spread, which increases the surface area of the body and therefore the lift.



Figure 8. Preening chest with the beak



thumbnail 1 : 0.000 s	thumbnail 2 • 0.044 s	thumbnail 3 : 0.1144 s
thumbnail 4 : 0.117 s	thumbnail 5 : 0.47 s	thumbnail 6 : 0.622
thumbnail 7 : 0.750	thumbnail 8 : 0.7 2 s	thumbnail 9 : 0.822 s

Figure 9. Preening chest and belly with the beak

Captions in Figure 9:

- **thumbnail 1**: the swift is stabilizing in gliding flight with its tail well spread out;
- **thumbnail 2**: the bird tilts its head forward;
- **thumbnail 3**: he begins grooming the chest feathers;
- **thumbnail 4**: he gradually lowers his head towards the belly;
- **thumbnail 5**: he grooms the belly feathers. The legs come out of the ventral plumage;
- **thumbnail 6**: he grooms the belly feathers;
- **thumbnail 7**: the head gradually returns to its first position;
- **thumbnail 8**: the legs start entering the ventral plumage;
- **thumbnail 9**: the bird keeps on gliding.

Grooming average time

Taking as limits of behavior the beginning and end of the head-to-breast shift, from the 21 shots studied, grooming average time was 1.00 s.

Video

Behavior frequency

From 153 preening events recorded in flight, 21 concerned breast and belly grooming, that is 13.72 % of the total (Table 2).

Discussion

Among 153 grooming behaviors recorded in flight, the 21 concerning chest and belly grooming represent 13.72% of the total.

Comparison between back and chest/belly grooming

Similarities

- 1. Both behaviors last the same average time of 1.00 s. These are therefore very brief postures that are very difficult to observe in detail at normal speed.
- 2. In both behaviors, the bird glides with wings and tail spread, seeking to maintain the inclination of the frontal plane at or near 0° to the horizon (TIGGES, 2004). In both behaviors, on the more detailed views, the bird closes its eyes.

Differences

- Chest grooming seems to be easier for the swift than back grooming. One difference is that the bird systematically keeps the wings fixed, spread out and symmetrical, while in the back grooming, the wings can move not necessarily in a symmetrical way. On the Figure 8, the bird does not even spread the tail feathers.
- 2. Since the bird can maintain a more efficient glide flight reducing altitude loss, the climb flight in preparation for chest grooming could be reduced or even be absent.

One shot (**Figure 10**) shows that the bird can chains in 4.35 s:

- 1. one back grooming (1.00 s)
- 2. one prey capture (0.033 s)
- 3. one chest grooming (1.10 s)

Comparaison with Alpine Swift

I filmed 3 chest grooming behaviors in the Alpine Swift (**Figure 11**). As with back grooming, this species shows the same postures and movements as those described in the Common Swift. The average time of this grooming (1.33 s) is 33% longer than in the Common Swift (1.03 s), certainly for the same reasons of larger size.

Larger dimensions provide better lift, and therefore less altitude loss when the bird stops flapping its wings during grooming.

Comparaison with others species

The ability to groom the ventral side (chest, axillaries, belly) in flight seems to be shared by a number of bird species as shown by these images found on the Web. (Figure 12).

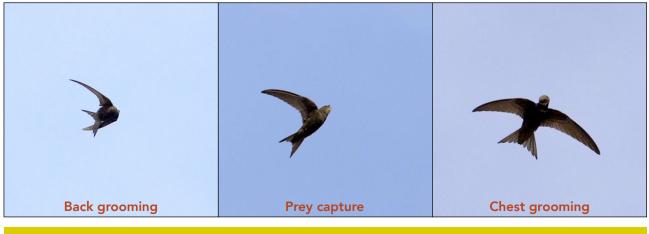


Figure 10.

Quick sequence of 3 behaviors : back grooming, prey capture, chest grooming



Figure 11.

Three pictures from videos of Alpine Swift grooming its chest in flight





Figure 12.

Twelve examples of pictures of birds grooming their backs

- 1 : Common House Martin (Delichon urbicum)
- 2 : Black-headed Gull (Chroicocephalus ridibundus)
- 3 : Black-legged Kittiwake (Rissa tridactyla)
- 4 : Ring-billed Gull (Larus delawarensis)
- 5 : California Gull (Larus californicus)
- 6 : Black Skimmer (Rynchops niger)
- 7 : Northern Gannet (Morus bassanus)
- 8 : Masked Booby(Sula dactylatra)
- 9: Magnificent Frigatebird (Fregata magnificens)
- 10 : Great Frigatebird (Fregata magnificens)
- 11 : Great Cormorant (Phalacrocorax carbo)
- 12 : Shy Albatross (Thalassarche cauta)

To watch these pictures on the Web, click on thumbnails (Accessed on 25/11/2018

1.4. Grooming legs with the beak



Figure 13. Legs grooming with the beak

Captions in Figure 13 :

- **thumbnail 1**: the swift is gliding with tail feathers widely spread;
- **thumbnail 2**: the bird tilts its head down, while its left leg comes out of the belly feathers;
- **thumbnail 3**: the bird's beak contacts the leg;
- **thumbnail 4**: on the video, the movements of the bird's head and the fixity of the leg show that the bird musts clean its fingers with its beak;
- **thumbnail 5**: the bird stops grooming: the head and leg will each return to their first position.
- **thumbnail 6**: the bird switches from gliding to flapping flight.

Grooming time

The action lasts exactly 0.66 s.

Behavior frequency

Among 153 grooming behaviors recorded in flight, only 1 concerns leg grooming, i.e. 0.65% of the total (Table 2).

Discussion

In the head-scratching with the claws of one leg, the videos show the quick scratching movements of the leg on the head while here it is the head that moves slowly and explores the leg, probably for cleaning it.

Common swifts never capture nor handle prey with their legs which are most of the time folded up and hidden in the plumage of the belly. Legs may therefore become dirty only when the bird clings to a vertical support or when it enters and stays in a cavity for breeding..



2. Grooming with the legs claws

The Common Swift has short legs with 4 forward-facing fingers including sharp claws that allow hanging vertically on the roughness of a rock face or wall.

In flight, swifts' legs are usually invisible because they are folded into the belly feathers, to improve aerodynamics, just as the landing gear of an aircraft (see the picture page 7).

But the legs can get out of the plumage and be visible in various situations.

1. When the bird grabs onto a vertical wall or enters a nesting site with the legs projected forward to absorb the impact and hang the roughness.

On the left picture of the Figure 14,

an adult returns to the nest with the sublingual pouch full of prey to feed its chicks. The two legs are well out to hang on to the tiles. The 4 fingers with powerful claws are all directed forward, which is a characteristic feature in the Apus genre.

2. In very hot weather, the flying swift opens a little its beak and lets its legs hang down for **thermoregulation** (C. NEUMANN, 2016)

On the right picture of **Figure 14**, shot in Samoëns (Haute-Savoie, France), on July 14, 2010 at 11:49 am in very hot weather (> 86° F), the legs hanging out of the plumage and the beak slightly open are visible.



Figure 14. Left : exit of the legs to land; Right : exit of the legs for thermoregulation

3. During fights between individuals in flight, the aggressor's legs are thrown against the other bird to grab it most often by legs, sometimes by one wing.

On these 3 pictures of the **Figure 15**, the legs of both birds are hung up. The two birds fall as they spin, then separate a second later.

4. During certain grooming behaviors,

the bird gets out the legs that are shaking underneath it for no other apparent reason than **keeping its body in balance**.

These legs exits are commonly observed in grooming by contorting and rubbing.









As in any bird, the legs of the Common Swift can also be used **grooming**. Due to their small size, they can be used only for head and neck scratching.

Captions in Figure 16 :

- **thumbnail 1**: the swift is in flapping flight for positioning with the tail feathers spread out
- **thumbnail 2**: the bird switches to gliding flight, with its wings extended and the tail feathers spread;

- **thumbnail 3**: the bird takes its right leg and moves it towards the chest;
- **thumbnail 4**: the bird has tilted its head and scratches its right side with the claws;
- **thumbnail 5**: after scratching, the leg will fold under the belly feathers and the head will straighten up;
- thumbnail 6: the bird keeps on gliding.

thumbnail 1 : 0.000 s	thumbnail 2 : 0.683 s	thumbnail 3 : 0.788 s
thumbnail 4 : 2.111 s	thumbnail 5 : 2.127 s	thumbnail 6 : 2.433 s

Figure 16.

Head-scratching using the claws of the right leg



Video

Behavioral analysis

Like in the chest grooming:

- the bird is gliding with wings well stretched and tail wide spread;
- then he tilts his head and actively scratches it with the claws of one of the two feet

The high mobility of the head, which may rotate 180° in both directions, allows the claws to reach all parts of the head and neck and thus ensuring an energetic brushing of the feathers.

In the two previous pictures, as already mentioned, eyelids are closed when scratching the head. The reason is obviously to protect the eyes from any poorly adjusted claw blow.

Note that it is possible that the claws may be used in flight to scratch other parts of the underside, but no shot shows this clearly to date.

Grooming average time

On 20 shots taken between the leg being in and out, grooming average time was 1.25 s.

Behavior frequency

Of the 153 grooming behaviors recorded in flight, 20 concern this one, i.e. 13.07% of the total (Table 2).

Discussion

DEREK BROMHALL in **1980**. in his book Devil Bird, The Life of the Swift, page 53 writes about the grooming:

A swift has special problems in preening, different from other birds. Being continuously on the wing it cannot rest to groom itself ; its legs are so short that only with great difficulty can it scratch its head when in the nest, a difficulty presumably compounded when it is actually flying.

In flight, my videos show that swift fairly well succeeds in energetic brushing thanks to its flexibility and high capacity to stretch the neck and turn the head 180° in both directions.

On the 20 video shots and on the 2 pictures, it is obvious that the leg that scratches always extends under the wing.

There are two methods for head scratching in birds (see SIMMONS, K.E.L., 1957):

- either by stretching the leg over the wing (method over the wing or indirect method);
- or by bringing the foot forward under the wing (method under the wing or direct method).

All individuals of a species generally practice the same method.

In **2014**, in Volume 46 of Advances in the Study of Behavior, pages 137 à 149, PELLIS *et al.* provide a kind of synthesis of knowledge on this head scratching in birds. They present a cladogram of the main groups of birds by distinguishing 3 subsets:

- groups using the under-wing method;
- groups using the over-wing method;
- groups using both methods.

In this cladogram based on the authors' observations and publications on headscratching, Swifts are considered with the 2 closely related groups, the Nightjars and Hummingbirds which practicee the indirect method of scratching over the wing.

This classification contrasts with my results which show the exclusive use of the direct method for in-flight Common Swifts.

Where can this difference come from? In **1959**, NICE ET SCHANTZ wrote:

The following birds have been reported to scratch over the wing : Goatsuckers, swifts, hummingbirds (Haverschmidt).

The source is referenced : HAVERSCHMIDT, F. 1957 Head-scratching in birds. *Ibis*, 99 : 688 I think the authors of the cladogram directly reproduced the results published by Haverschmidt in 1957

These are presumably observations made at the nest with settled down birds .

Indeed, I filmed an individual at the nest who shows the passage of the leg over the wing (picture below). Other observations at the nest show that the Common Swift can use either method. (U. Tigges, personal communication, May 30, 2018)

Two groups of bird species, Swallows (BURTT *et al.* 1988) and Frigatebirds (KRAMER, 1964) are known to show variations in behavior depending on the context.

Thus several species of swallows exhibit the two methods of head scratching:

- when settled down or perched, they use the indirect method over the wing;
- in flight, they use the direct method under the wing.

According to authors, this is presumably related to the change in the position of the

gravity center in relation to the locomotor system, depending on whether the bird is perched or flying.

We can conclude as follows:

- in flight, Common Swift scratches its head and neck by systematically passing its leg under the wing;
- seated in the nest, Common Swift scratches its head and neck by passing its leg either over the wing or under the wing, depending on the situation.

It would be interesting to measure the frequency of both methods in juveniles and adults in the nest.

The image below is taken from an infrared video shot in a nest box entered by two swifts for exploring it as a possible nesting site.

The bird in the foreground scratches its head by passing its left leg over the wing. As already mentioned, the under-wing method was also observed in the nest.





Figure 17.

Head-scratching in-flight. Comparison with 4 other species.

Video

1. Alpine Swift (Tachymarptis melba): the bird scratches for 1.66 s the beak area by passing the left leg under the wing, in a posture quite comparable to that observed in the Common Swift (or it cleans its claws?)

2. Eurasian Crag Martin (*Ptyonoprogne rupestris*) : on this photograph, the bird scratches the underside of its head by passing its left leg under the wing in a position quite comparable to that observed in the Common Swift and Alpine Swift

3. **Cadwall** (*Mareca strepera*) : on the video of a pair of Gadwalls, filmed in slow motion, the female scratches her head underside and upper chest by passing her right leg under the wing and then shakes the head with rapid rotations of the neck. Grooming lasts 3 seconds and is done in flapping

4. **Common Tern** (*Sterna hirundo*) : on a video of a Common Tern, filmed in slow motion, the first two images show that the bird rising before turning the head to scratch. Grooming is done in gliding flight without flapping wings, the bird losing altitude. At the end of the behavior the bird returned to the same distance from the water surface as at the beginning. The head-scratching lasts 1.8 seconds and is done by passing the left leg under the wing.





Figure 18.

Ten examples of pictures of birds in flight scratching their heads with a leg

- 1 : Chimney Swift (Chaetura pelagica) in flight using the under the wing method
- 2 : Hirondelle rustique (Hirundo rustica) when perched using the over the wing method
- 3 : Barn Swallow (Hirundo rustica) in flight using the under the wing method
- 4 : Red-rumped Swallow (Cecropis daurica) in flight using the under the wing method
- 5 : Common House Martin (Delichon urbicum) in flight using the under the wing method
- 6: White-winged Tern (Chlidonias leucopterus) in flight using the under the wing method
- 7 : Bridled Tern (Onychoprion anaethetus) in flight using the under the wing method
- 8 : Royal Tern (Thalasseus maximus) in flight using the under the wing method
- 9: Northern Gannet (Morus bassanus) in flight using the under the wing method
- 10: Brown Pelican (Pelecanus occidentalis) in flight using the under the wing method

To watch these pictures on the Web, click on thumbnails (Accessed on 25/11/2018

Comparative study

Figures 17 and **18** show that all these species, filmed or photographed in flight, use the direct method for head-scratching by passing the leg under the wing, regardless of the method usually used when individuals of the species are posed or perched.

Passing the leg over the wing must raise a balance problem that is too complicated to manage for a bird in flight.

This scratching is mainly done in gliding flight, with wings well spread, but the example of the Gadwall also shows that it can occur during a flapping flight.

3. Grooming by contorting, rubbing, wing fluttering, rolls

These behavioral items are visible in 41 videos and may be interpreted as an energetic grooming of the entire plumage

3.1. Grooming by contorting and rubbing

In 34 videos, after a typical gliding flight preceding a grooming sequence (see previous descriptions), the bird rubs the wings on the spread tail and then folds them along the body and rubs them vigorously against each other, on its back and tail with twists and turns.

Captions in Figure 19:

- **thumbnail 1**: the Swift is gliding with fully spread tail feathers. The 2 legs coming out of the ventral feathers are hanging.
- **thumbnail 2**: after twisting to the right, it twists to the left of the spread tail, with the underside of the left wing rubbing against the tops of the rectrices;
- **thumbnail 3**: while crossing the undersides of the 2 wings rub the feathers of the back and the top of the tail feathers;
- **thumbnail 4**: the undersides of the 2 wings while crossing rub the feathers of the back and the top of the tail feathers;
- **thumbnail 5**: the bird tilts about 150° to the right and shows its ventral side. Feathers of the 2 wings are strongly released. Then he will do the same to the left;
- **thumbnail 6**: the bird returns, continues gliding flight, with feathers having recovered their cohesion.



Figure 19. Grooming by contorting and rubbing (side view) **Figure 19** shows the bird in profile. On the second case the bird is seen full face

Captions in Figure 20:

- **thumbnail 1**: in gliding flight, the bird takes out the legs, shakes from left to right, with the tail spread out;
- **thumbnail 2**: the bird keeps gliding and spreads out the rectrices as much as possible;
- **thumbnail 3**: the bird twists its tail to the right;
- **thumbnail 4**: the bird twists its tail to the left;
- **thumbnail 5**: while crossing the undersides of the 2 wings rub the back feathers and the top of the tail feathers;
- **thumbnail 6**: while crossing the undersides of the 2 wings rub the back feathers and the top of the tail feathers;

- **thumbnail 7**: while crossing the undersides of the 2 wings rub the back feathers and the top of the tail feathers;
- **thumbnail 8**: while crossing the undersides of the 2 wings rub the back feathers and the top of the tail feathers;
- **thumbnail 9**: the bird swings to the right with its wings in a vertical plane;
- **thumbnail 10**: the bird returns to the starting position;
- **thumbnail 11**: while crossing the underside of the 2 wings rub again the back feathers and the top of the tail feathers;
- **thumbnail 12**: the bird recovers, retracts its legs, and then continues its gliding flight.

thumbnail 1 : 0.000 s	thumbnail 2 : 0.694 s	thumbnail 3 : 0.744 s	thumbnail 4 : 0.850 s
		A	
thumbnail 5 : 0.927 s	thumbnail 6 : 1.061 s	thumbnail 7 : 1.233 s	thumbnail 8 : 1.322 s
*			X
thumbnail 9 : 1.472 s	thumbnail 10 : 1.666 s	thumbnail 11 : 1.727 s	thumbnail 12 : 1.905 s
		i di seconda de la constante d	~

Figure 20. Grooming by contorting and rubbing (front view) Video

Behavioral analysis

During this acrobatic aerobatics the bird suddenly loses altitude without spinning. The movements of the wings, tail and legs keep the bird's body in a position close to that of the beginning of the aerobatics.

On the front view (**Figure 20**), alternating friction movements of the wings on the tail remind the swaying arms of a speed skater.

On the side view (Figure 19), at the beginning of the aerobatics the legs come out of the ventral plumage, stir but without interfering with grooming. Their exits and movements probably contribute to stabilize the bird's body.

On most shots where the behavior is completely exhibited, after the friction and crossings of the wings, the bird swings to the right and left while shaking the wings, whose wings feathers loose and move separately, as well as tail feathers.

This kind of shaking is probably used to get rid of dirt stuck to the plumage during the flight and/or in the nesting site (spider web on the tail of a swift).

These vigorous rubbings may also questionably be intended to dislodge parasites firmly attached to the bird's plumage or skin such as *Crataerina pallida*.



Grooming average time

On 34 shots, grooming average time was 1.34 s.

Behavior frequency

Of the 153 grooming behaviors recorded in flight, 34 concerned this one, i.e. 22.22 % of the total (Table 2).

Sequencing this behavior with other grooming behaviors

On some videos, this behavior may follow other forms of grooming such as back grooming.

Discussion

In **1968**, , this behavior was first described by OEHME, was named « flattersturz » which can be translated as « fluttering fall » and described it as follows:

Der Segler fliegt noch eben geradeaus, plötzlich wirbelt er, eigenarig mit den Flügeln schlagend, abwärts, fängt sich ebenso rasch und fliegt weiter. Das Ganze kann sich wiederholen, der Vorgang sebst verläuft außerordentlich rasch (Abb. 4 umfaßt ½ s!). Der Ablauf war bei 3 gefilmten Flugmanövern dieser Art immer gleich.

A quotation that can be translated as:

The swift flies straight ahead, suddenly whirls, strangely flapping its wings, downwards, and catching itself just as fast and flies on. The whole process can be repeated, and proceeds astonishingly quickly (Fig. 4 includes ½ s!). The procedure was always the same with 3 filmed flight manoeuvres of this kind.

At the end of his article, which also analyses inverted flight (upcoming study in a forthcoming paper), OEHME provisionally concluded:

Uber die Rolle des Rückenfluges und des Flattersturzes im Leben des Seglers läßt sich kaum etwas Bündiges aussagen. Als besondere Flugweisen für den Nahrungserwerb können sie kaum aufgefaßt werden. Gegen die Annahme, es seien Bestandteile des Fortpflanzungsverhaltens, spricht, daß sie während des ganzen Sommers, auch nach dem Ausfliegen der Jungvögel, beobachtet

werden können. Es bliebe die Möglichkeit, daß der Segler mit solchen Flugtechniken einen verfolgenden Feind (z. B. Baumfalken) ausmanövrieren kann. Aber darüber sind bis jetzt keine Beobachtungen bekannt.

A quotation that can be translated as: Hardly anything can be said on the role of the inverted flight and the fluttering fall in the life of swifts. As special flight-ways for foraging, they can hardly be understood. Against the hypothesis that they are components of the reproductive-behaviour, is the fact that they can be observed during the whole summer, even after the young fledged. However it may be that the Swift can outmaneuver a pursuing predator (for example Hobby) using such flight-techniques. But there are no known observations about this so far.

1968, Oehme does not suggest In grooming behavior, it focuses more on the aerodynamic characteristics of the various flights of the Common Swift than on their biological significance.

In 1973, G. Rothgänger & H. Rothgänger take up OEHME's description above and continue their analysis of this behavior.

Bei unseren Beobachtungen hatte es den Anschein, daß der Segler kopfüber, um die Längsachse drehend zur Erde stürzte (visuelles Beobachten). Oehme (1968a) konnte durch Luftbildaufnahmen nachweisen, daß keine schraubenförmige Drehung erfolgt, sondern die Flügel passiv wie ein Windrad bewegt werden. Der Flattersturz ist gleichfalls eine Säuberungshandlung, die häufig nach mehrmaligem Kopfwenden ausgeführt wird. Vermutlich wird der Parasit in diesem Fall nicht mit dem Schnabel erreicht (Crataerina pallida hält sich verstärkt in der Hals- und Kopfregion auf. Büttiker 1944). Die Entfernung erfolgt durch passives Flügelschlagen.

A quotation that can be translated as: During our observations it seemed that the swift fell down upside, turning around the longitudinal axis towards the ground (visual observation). Oehme (1968a) has shown from aerial photographs that no helical rotation takes place, but that the wings moved passively like a windmill. The fluttering fall is also a cleaning action, which is frequently carried out after several head turns*. The parasite is presumably not reached in this case with the beak (Crataerina pallida mostly stays intensively in the neck and head region) (Büttiker 1944). The removal is done by passive flapping of the wings

*head turns : Indeed on two of my videos this behavior is preceded by fast twisting movements of the head.

In 1973, G. Rothgänger & H. Rothgänger are therefore the first to consider this behavior as in-flight grooming.

1998, YVES GARINO described In а similar behavior that he described as "deparasiting flight":

L'oiseau ébouriffe son plumage et ferme ses ailes, qu'il frotte l'une contre l'autre. Très souvent, au cours de la chute consécutive à la fermeture des ailes, l'oiseau effectue deux ou trois tours sur lui-même (tonneaux), puis il reprend son vol normal. Les jours sans vent, on entend des bruits d'ailes difficiles à transcrire lors de cette manœuvre.

A quotation that can be translated as:

The bird ruffles its plumage and closes its wings, which it rubs against each other. Quite often, during the drop following the closing of the wings, the bird makes two or three turns on itself (roll over), then it resumes its normal flight. On windless days, wing noises can be heard but they are difficult to transcribe during this manoeuvre.

In his references, GARINO does not report the work of OEHME nor that of G. Rothgänger & H. Rothgänger. One can only notice that the bird does not roll over, which was something the German authors had noticed. For wing noises, slow motion



videos do not record sound.

In **2012**, on Youtube, a **vidéo** shows at 18 s, such behavior filmed at normal speed.

In **2017**, CÉCILE PICHOT described this behavior as "flight with the wings folded":

Le vol avec les ailes repliées (replié) (fig. 3.4) est quant à lui un vol sans propulsion ni portance, lors duquel l'oiseau peut soit plier les ailes pour les plaquer contre le corps (fig. 3.4a), soit mouvoir passivement les ailes dans tous les sens de manière asynchrone et asymétrique (fig. 3.4b).

A quotation that can be translated as:

Flight with the wings folded (folded) (fig. 3.4) is a flight without propulsion nor lift whereby the bird can either fold the wings to press them against the body (fig. 3.4a) or move them passively in any direction in an asymmetrical and asynchronous manner (fig. 3.4b).

It should be noticed that as Yves GARINO, she does not mention in her reference list the works of OEHME and G. ROTHGÄNGER & H. ROTHGÄNGER.

In page 29, she clarifies:

Vol avec les ailes repliées

[Vol sans portance ni propulsion]

Les ailes n'exercent à priori aucune portance et peuvent être dans deux positions :

- Les ailes sont collées au corps et peuvent se croiser. L'envergure est minimale (proche de la largeur du corps). Cette position peut être maintenue sur plusieurs images.

- Les ailes sont décollées du corps, voir complètement ouvertes, et ne sont pas symétriques. Cette position n'est pas maintenue...

A quotation that can be translated as:

Flight with the wings folded

[Flight without lift or propulsion]

The wings do not exert any lift and can stand in two positions:

- They are plated to the body and may cross each other. The wingspan is minimal (close to the width of the body). This position can be maintained on several images.

- They are detached from the body, or even completely open, and are not symmetrical. This position is not maintained...

This posture corresponds to the first stages of the behavior when the bird rubs a wing on the tail feathers successively to the right and then to the left. The second posture corresponds to the following steps when the bird crosses both wings several times on its back.

About the Flight with the wings folded (page 22 and 23), she says:

Des explications possibles de ce vol seraient que l'oiseau pourrait soit capturer une proie et ensuite la manipuler, soit faire du toilettage. Replier les ailes peut alors lui permettre de se contorsionner plus facilement, ou encore de se concentrer sur sa tâche (e.g. toilettage, manipulation de proie) et non plus sur le vol.

A quotation that can be translated as:

Possible explanations for this theft would be that the bird could either capture a prey and then handle it, or groom it. Folding the wings back can then allow it to twist more easily, or to concentrate on its task (e.g. grooming, handling prey) and no longer on flying.

To my knowledge, birds that hunt small insects in flight (Swifts, Swallows,...) do not handle their prey in flight.

From the 348 shots of potential capture I filmed, the Swift's beak opens and closes on the prey.

Here, this is a grooming behavior having nothing to do with capturing prey.

85

Comparaison with Alpine Swift

I filmed 2 videos where the bird shows a grooming by contortions with rubbing, in a series of postures quite comparable to those observed in the Common Swift. (Figure 21 and Figure 22).

In the Alpine Swift, the average time of grooming by contorting and rubbing is 1.40 s, which is very close to that found in the Common Swift (1.34 s).

thumbnail 2 : 0.133 s	thumbnail 3 : 0.572 s
thumbnail 5 : 1.266 s	thumbnail 6 : 1.522 s
	~

Figure 21. Alpine Swift. Grooming by contorting and rubbing

thumbnail 1 : 0.000a s	thumbnail 2 : 0.133 s	thumbnail 3 : 0.427 s
*		~
thumbnail 4 : 0.883 s	thumbnail 5 : 1.050 s	thumbnail 6 : 1.327 s
¥	64	
	le l	

Figure 22. Alpine Swift. Grooming by contorting and rubbing

Video

Video



Figure 23. Top : Western Marsh Harrier (*Circus aeruginosus*) Bottom : Eurasian Hobby (*Falco subbuteo*)

Comparaison with other species

In two species of birds of prey, I filmed elusive behaviors similar to those of the Swifts.

Western Marsh Harrier (*Circus aeruginosus*) A Western Marsh Harrier, filmed in slow motion in flight, shows a kind of energetic grooming of the entire plumage (**Figure 23 Top**). For 1.16 s, the bird seen backside is gliding and lets the legs hanging down, then rubs the half-folded wings one on top of the other.

Hobby (Falco subbuteo)

A shot of a Hobby, filmed in flight in slow motion, shows a kind of energetic grooming of the entire plumage. The bird seen from below is gliding up in a thermal lift. Suddenly, it produces 3 vigorous flaps of the wings which it folds backwards, with the legs hanging. It shakes the wings by rubbing them on the back and the tail wide open. Then it resumed its gliding flight. This in-flight grooming lasted only 1 second.

For the Common Swift, I did not find any images of this behavior on the Web except these two pictures (**Figure 24**) that the German author describes as "skurriles" that can be translated by "weird, strange, unusual".





Figure 24. Common Swift To see these pictures on the Web, click on thumbnails (Accessed on 25/11/2018)

3.2. Grooming by wing fluttering

thumbnail 1 : 0.000 s	thumbnail 2 : 0.483 s	thumbnail 3 : 0.522 s	thumbnail 4 : 0.555 s
	Ø		Ø
thumbnail 5 : 0.605 s	thumbnail 6 : 0.638 s	thumbnail 7 : 0.683 s	thumbnail 8 : 0.722 s
	-19		1
thumbnail 9 : 0.766 s	thumbnail 10 : 0.883 s	thumbnail 11 : 1.038 s	thumbnail 12 : 1.222 s
		\mathbf{i}	

Figure 25. Grooming by wings fluttering

Captions in Figure 25 :

- **thumbnail 1**: swift in gliding flight changes to a flapping flight of high amplitude;
- **thumbnail 2**: it lowers its wings sharply without making them touching each other;
- **thumbnail 3**: the wings rise up in dihedral;
- **thumbnail 4**: it lowers its wings sharply again up to crossing them;
- **thumbnail 5**: the wings are raised in dihedral as in thumbnail 3;
- **thumbnail 6**: it lowers its wings sharply again to the point of making them touching;
- **thumbnail 7**: the wings are raised in dihedral as in thumbnails 3 and 5;

• **thumbnail 8**: it lowers its wings sharply to the point of making them touching;

Video

- **thumbnail 9**: the wings are raised in dihedral as in thumbnails 3, 5 and 7;
- **thumbnail 10**: the wings fold and cross on the back;
- **thumbnail 11**: the bird swings to the right, with the wings stretched with theirs feathers released;
- **thumbnail 12**: it continues its gliding flight.

Behavioral analysis

On 5 videos, during a gliding or flapping flight, the Swift starts to produce, with a high amplitude fluttering of both wings: 4 flutterings in each of the three shots of 2017; 5 flutterings in one of the two shots of 2018. The study of **Figure 25** shows the wings seeming to touch each other in the lower position as if it was « clapping «, but not in the upper position where the wings form a 90° angle (as in the dihedral flight position). After these fluttering actions, it starts swinging to the right and left two or three times with its loose wing feathers that shake separately as at the end of the grooming by contorting and rubbing.

Grooming average time

On the 4 shots that show the complete behavior, the average time of the grooming by wing fluttering is 0.82 s.

Behavior frequency

Of the 153 grooming behaviors recorded in flight, 5 concern this one, i.e. 3.27% of the total (Table 2).

Discussion

Like the previous one, this behavior should also contribute to rid the bird of dirt and maybe of parasites such as *Crataerina pallida* although this is more difficult.

Could it be also a territorial display, a social behavior of the type « Wing-clapping » ? as described on page 663 of *The Birds of the Western Palearctic*, Vol. IV. (CRAMP, 1985):

Flying birds often perform Wing-clapping : wings meet over back, producing clapping

sound, then quickly lowered until they meet below body. May be repeated several times (once, c. 6) in rapid succession (BUNDY 1975).

From the 5 video studied, if the wings really touch in the lower position, they are far from doing so in the upper position: thumbnails 3, 5, 7 and 9 in **Figure 25** show that the angle formed between the wings is then close to 90°.

This behavior could therefore have two functions, social and hygienic.

Comparaison with Sand Martin (*Riparia riparia*)

A Sand Martin in flight, filmed in slow motion, shows a kind of energetic grooming of the entire plumage (**Figure 26**).

The bird is gliding against the wind. Suddenly, it produces 3 energetic and loose wings flutterings, without the wings touching above and below the body. The bird swings to the right and then to the left twice in a row, fluttering its wings with the wing feathers loosened. This in-flight grooming lasted only 0.8 s and ended with 2 head rotations.









3.3. Grooming by rolls

thumbnail 1 : 0.000 s	thumbnail 2 : 0.027 s	thumbnail 3 : 0.055 s	thumbnail 4 : 0.083 s
X			X
thumbnail 5 : 0.111 s	thumbnail 6 : 0.138 s	thumbnail 7 : 0.166 s	thumbnail 8 : 0.194 s
		K	
thumbnail 9 : 0.222 s	thumbnail 10 : 0.250 s	thumbnail 11 : 0.277 s	thumbnail 12 : 0.305 s
		*	
thumbnail 13 : 0.333 s	thumbnail 14 : 0.361 s	thumbnail 15 : 0.388 s	thumbnail 16 : 0.405 s
	K		
thumbnail 17 : 0.444 s	thumbnail 18 : 0.472 s	thumbnail 19 : 0.500 s	thumbnail 20 : 0.527 s
	F		
Figure 27.			Video



In 2 shots the bird rolls 3 times right-leftright at almost 180°, the wings stretched with the feathers released. (Figure 27).

Grooming average time

For these 2 videos, the grooming average time was 0.67 s.

Behavior frequency

Of the 153 grooming behaviors recorded in flight, 5 concern this one, i.e. 3.27% of the total (Table 2).

Discussion

As with the two previous behaviors, one may assumed that these aerial acrobatics help the bird eliminating dust and possibly parasites from the plumage.

It should be noticed that, for the first time, the bird is shown finding itself for a fraction of a second with its body in an inverted position with the head almost facing the sky. (**Figure 27**, thumbnail 11). The head partly follows the rotation of the bird's body, while in reverse flight, the bird rotates the body 180° but most often tries to keep the head in its initial and normal flight position (see the study of flights in a future paper).

A roll of almost 180° with strong fluttering can also be observed at the end of some grooming by contorting and rubbing as shown in the **Figure 28**.

Captions in Figure 28.:

- **thumbnails 1 to 5**: typical postures of the grooming by contorting and rubbing;
- thumbnails 6 to 9: the swift ends with a 180° roll pattern which is quite comparable to that described in the Figure 27.

thumbnail 1 : 0.000 s	thumbnail 2 : 0.588 s	thumbnail 3 : 1.055 s
	The second secon	A
thumbnail 4 : 1.116 s	thumbnail 5 : 1.255 s	thumbnail 6 : 1.300 s
thumbnail 7 : 1.311 s	thumbnail 8 : 1.327 s	thumbnail 9 : 1.538 s





4. Behaviors that may be related to grooming

4.1. Head rotation with closed beak

On 5 shots, the bird makes one or two very fast head rotating twists, left and right, with an amplitude of up to 180°, with the beak closed. These rotations concern only the head. In 2 of these 5 shots, they precede by 1 to 2 seconds a grooming by contorting and rubbing.

This sequence had already been identified by G. Rothgänger & H. Rothgänger en 1973.

> Der Flattersturz ist gleichfalls eine Säuberungshandlung, die häufig nach mehrmaligem Kopfwenden ausgeführt wird.

A quotation that can be translated as:

Falling while flying is also a cleaning action, which is often performed after several head rotations.

Captions in Figure 29 :

- thumbnail 1: the bird is gliding;
- **thumbnail 2**: the bird rotates its head 180° to the right;
- **thumbnail 3**: back to the first position;
- **thumbnail 4**: the bird rotates its head to the left;
- **thumbnail 5**: the bird rotates its head 180° to the left;
- thumbnail 6: back to the first position;
- **thumbnail 7**: back to the first position;
- **thumbnail 8**: the bird rotates its head 180° to the right;
- **thumbnail 9**: back to the first position.

thumbnail 1 : 0.000 s	thumbnail 2 0.011 s	thumbnail 3 :0.022 s
thumbnail 4 : 0.033 s	thumbnail 5 : 0.050 s	thumbnail 6 : 0.061 s
thumbnail 7 : 0.072 s	thumbnail 8 : 0.094 s	thumbnail 9 : 0.111 s

Figure 29. Head rotation with closed beak



Grooming average time

For these 5 shots, the grooming average duration is 0.16 s.

Behavior frequency

Of the 153 grooming behaviors recorded in flight, 5 concern this one, or 3.27% of the total (Table 2).

Discussion

These very fast twists of the head can be used to push out dirt or remove parasites. In **1980**. DEREK BROMHALL, on page 53 in his book *Devil Bird*, the life of the Swift described very fast head vibrations at the nest.

As well as panting and yawning the swifts occasionally vibrated head and beak very rapidly, for no more than two or three seconds at a time. Such behavior, which occurs during the course of preening sessions in the nest, has no previously been reported. The vibration was so rapid, and was over so guickly, that it was difficult to be sure it had actually happened; in fact, we were uncertain ourselves until we closely examined the film recording the event. What at first appeared to be a blurred and out-of-focus sequence of the swift's head proved, on analysis of the film, frame by frame, that the bird was in fact vibrating its beak and head at such a speed that the image on the film appeared as a blur. We later found that a photograph taken at 1/1000 second exposure was still too slow to freeze the movement of the head.

An explanation of such curious behavior can only be tentative. It could be to dislodge parasites on the head, and perhaps in the nostrils, where mites congregate, but if so it has no effect that one can observe. More likely, in my view, is that it is means by which the swift preens that part of his body which it cannot reach at all with his beak, and only very awkwardly and inefficiently with his claws. By vibrating the head at high speed, individual feathers separate, small particles of dirt and debris are shaken off and the feathers fit neatly into place again when the vibration ceases. A swift has special problems in preening, different from other birds. Being continuously on the wing it cannot rest to groom itself; its legs are so short that only with great difficulty can it scratch its head when in the nest, a difficulty presumably compounded when it is actually flying. One might suppose also that swifts have a particular need to groom the feathers of the head. They catch several thousand insects each day, many of which are soft-bodied and easily damaged on impact with a swift travelling at high speed; it is to be expected that insect juices and small fragments, as well as the swift's own saliva, will adhere to the feathers around the beak and head. Indeed, this can be seen when swifts which are feeding chicks bring back food in their throat pouches. It is possible that while on the wing the swift cleanses and grooms the feathers of his head by vibrating them at high speed, in a manner similar to the way we use ultra-sonic vibration to clean clothing. What we observed as a rare event in the nest-box may normally occur while the bird is in flight.

Two comments about this quotation.

- 1. My videos show that the Swift is quite able to scratch its head in flight as well as in the nest.
- 2. In my videos, it is not really a matter of head vibrations but of fast and high amplitude rotations.

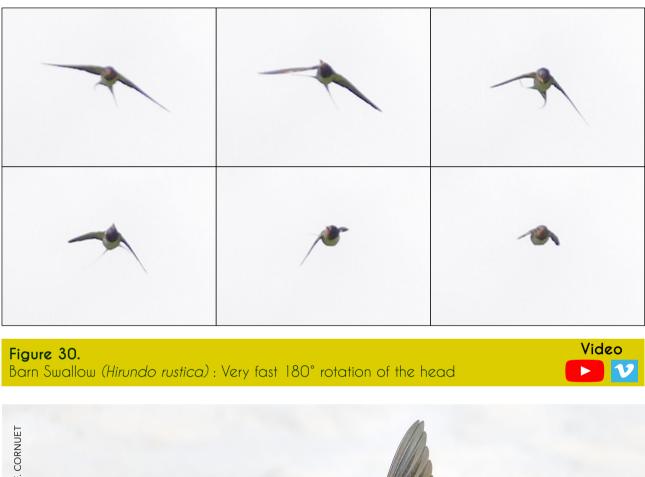


Comparaison with the Barn Swallow (Hirundo rustica)

A shot of an adult Barn Swallow in flight shows such a behavior of very fast head rotations.

With the beak closed, the bird rotates very quickly 180° to the right, left and again to

the right. The total action lasts 0.100 s. This shot is part of a series on Swallows hunting low-rise insects in a meadow (Figure 30).







Comparaison with Sandwich Tern

Most diving birds, such as the Sandwich Tern, shake when getting out of the water while rotating their heads very quickly. (Figure 31).

Generalization

These very fast head rotations are regularly observed in birds perched or seated during grooming, diving, swimming, and dust bathing. They are used to remove water droplets, solid particles, possibly parasites if they are not firmly attached to the feathers or fixed on the skin (ticks...).



Figure 31. Sandwich Tern (Thalasseus sandvicensis): Very fast 180° rotation of the head





quickly right and left. (Figure 32).

4.2. Head rotation with open beak

On 5 videos the bird opens its beak wide with its tongue floating. He twists its head very

thumbnail 1 : 0.000 s	thumbnail 2 : 0.011 s	thumbnail 3 : 0.022 s
thumbnail 4 : 0.033 s	thumbnail 5 : 0.044 s	thumbnail 6 : 0.055 s
thumbnail 7 : 0.066 s	thumbnail 8 : 0.077 s	thumbnail 9 : 0.088 s
thumbnail 10 : 0.099 s	thumbnail 11 : 0.111 s	thumbnail 12 : 0.122 s
thumbnail 13 : 0.133 s	thumbnail 14 : 0.144 s	thumbnail 15 : 0.155 s

Figure 32. Head rotation with open beak





Behavioral analysis

It differs from the previous behavior by two characteristics:

- The bird opens its beak wide with its tongue floating or not. Eyes are closed with the large eyelids as is often the case when a Common Swift opens its beak widely (see the upcoming paper on prey catches);
- The head twists are more energetic than in the previous case: they involve the whole body to the point that the tail, with its fan-shaped feathers, also makes a twist.

In 2 shots of 2018, the behavior is preceded by a catch; only one of these shots shows the rejection of the caught prey. (**Figure 33**).

Captions in Figure 33 :

- **thumbnail 1**: the prey is spotted, the swift is ready for a catch;
- **thumbnail 2**: the head is projected forward, with the beak wide open;
- thumbnail 3: the prey is caught;
- **thumbnail 4**: the prey is inside the mouth;
- **thumbnail 5**: the swift immediately rejects the prey by opening the beak wide and turning the head very quickly;
- **thumbnail 6**: the swift rejects the prey by keeping the beak wide open;
- **thumbnail 7**: the swift rejects the prey by keeping the beak wide open;
- **thumbnail 8**: the swift rejects the prey by keeping the beak wide open;
- thumbnail 9: the swift closes its beak

Did the insect sting the Swift's mouth?

thumbnail 1 : 0.000 s	thumbnail 2 : 0.005 s	thumbnail 3 : 0.011 s
*	-	-
thumbnail 4 : 0.172 s	thumbnail 5 : 0.205 s	thumbnail 6 : 0.211 s
4	A.	7.
thumbnail 7 : 0.233 s	thumbnail 8 : 0.238 s	thumbnail 9 : 0.266 s
1.	1.	T,

Figure 33. Capture and prompt rejection of a prey





Grooming average time

In the shot where the behavior described on the **Figure 32**, the swift shows, within 1.66 s, 4 rotations which have exactly the same duration (0.155 s) and which follow the same sequence of postures.

In the example of the **Figure 33**, the bird has its beak open for 0.066 seconds, the time to reject the prey immediately after having caught it.

Behavior frequency

Of the 153 grooming behaviors recorded in flight, 5 concern this one, or 3.27% of the total (Table 2).

Discussion

When hunting for itself, the Common Swift immediately ingests the insects it catches. The example of the **Figure 33** shows that the bird, in certain circumstances, can immediately reject the prey. In papers on the Common Swift, it is generally recognized that the bird can select its prey on sight before capture. For example, the swift is mentioned for its ability to select stingless drones while avoiding the capture of worker bees who are equipped with them. (Lack, 1956).

The **Figure 33** shows that selecting of a prey can be made exceptionally by its prompt

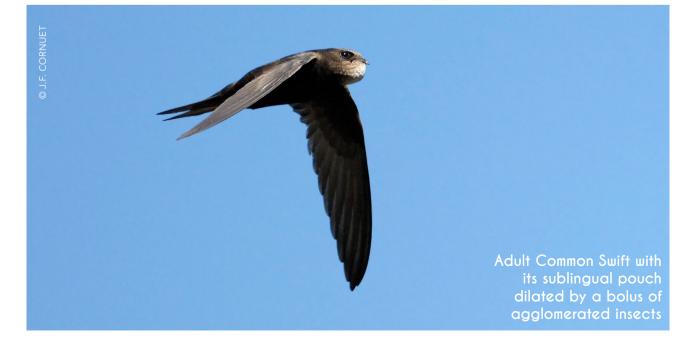
rejection after a catch.

This seems to me to be a very rare and accidental behavior in view of the hundreds of captures filmed without visible rejection. When feeding its chicks, Common Swift hunts several hundreds, often small prey, which it swallows with saliva and stores alive as a bullet or bolus in a sublingual pouch (photo below). At the nest, he regurgitates this bolus in the mouth of a chick.

It is then possible that after feeding, when leaving the nest, the bird will find it necessary to clean its mouth by shaking its head vigorously with its beak wide open.

The Common Swift can also clean its mouth cavity when **it takes water by skimming the surface with its beak wide open.** The often repeated passages suggest that they are not only used to satisfy thirst (U. Tigges, personal communication).

Finally, it should be noted that there are no reliable data have so far been reported on rejection pellets by the Common Swift. (U. Tigges, personal communication).





5. Review

Grooming in flight is challenging for the Common Swift because the bird must:

- groom all body parts correctly;
- limit altitude loss;
- maintain a good perception of the environment during grooming.

This analysis shows different strategies developed by the Common Swift to face these 3 challenges.

5.1. Grooming all body parts properly

Head

Thanks to its very mobile head and strong claws the bird can scratch all parts of the head. Quick twists of the head with the beak closed complete external grooming. fast twisting with a wide open beak can ensure the mouth hygiene.

• Trunk

Head mobility and neck extension allow the beak preening chest, belly and back feathers.

• Legs

The bird's flexibility allows it cleaning the legs with the bill.

• Tail

The neck extension and the arch of the bird's back capabilities are used to preen the tail feathers and access the uropygeal gland for plumage maintenance.

Tail feathers also benefit from grooming by contorting and rubbing.

• Wings

The long wings are mainly maintained during contorting grooming with the release of strongly shaken feathers and rubbing of the wings on each other, on the tail and the back.

5.2. Limiting altitude loss

All in-flight grooming actions are accompanied by loss of altitude.

For limiting altitude loss, the bird uses three complementary strategies:

- gain altitude before grooming begins;
- reduce altitude loss by increasing lift;
- reduce grooming time.

1. Gain altitude before starting grooming

Several shots show a short ascending flight before groomin starts. This elevation can be achieved by a particular potentially ascending flapping flight with tail feathers widely spread. Swifts also know how to take advantage of thermal updrafts to glide upwards (HEDRICK, PICHOT ET DE MARGERIE, 2018).

2. Reduce altitude loss by increasing lift

Grooming with beak and claws is always done during a gliding flight whereby wings and tail are widely spread for increasing the surface area and therefore the lift. The bird slows down its descent and reduces altitude loss.

From the posture studies, one may classify behaviors according to the exepted amount of altitude loss (**Figure 34**, **Figure 35**, **Figure 36**).





Figure 34.

Chest grooming (L) and head-scratching (R) while the bird succeeds to maintain the initial spread position of gliding flight presumably cause limited altitude loss.

Figure 35.

Backwards head rotation while back grooming (L) as well as back bending while tail feathers preening (R) reduce body area, which increase altitude loss.

1

Figure 36.

Cross movements of the wings on the back (L) and wing and tail feathers relaxation (R) probably cause the most important altitude loss of all the studied behaviors.

Table 4.

Average time for grooming behaviors studied in the Common Swift

	Number of data processed	Average time (second)				
Back	57	1.00				
Tail feathers	2	1.3 3				
Chest and belly	21	1.00				
Legs	1	0.66				
Head-scratching	20	1.25				
Contorting and rubbing	34	1.34				
Wings fluttering	4	0.82				
Rolls	2	0.67				
Head rotation with closed beak	5	0.16				
Head rotation with open beak	1	4 rotations of 0.155 s in 1.66 s				

3. Reduce grooming time

To reduce altitude loss, Common Swift also chose for very short grooming times (Table 4).

In-flight grooming average times last one or less than one second.

This shortness is one of the main reasons why these behaviors have so far been little studied in detail. Only a very slow motion video at close range provides a detailed description of these behaviors.

5.3. Perception of the environnement during grooming

In all grooming behaviors studied, despite the acrobatic postures necessary to reach the different parts of the body, the bird permanently tends to maintain the inclination of the frontal plane at or near 0° relative to the horizon (Tigges, 2004) using coordinated movements of the wings, legs and tail.

6. Behavioral dataset



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In-flight grooming in the Common Swift - Behavioral dataset



The **Figure 37** shows a first behavioral dataset of in-flight grooming in the Common Swift. Based only on shots taken at a fixed location near a small urban colony, it is necessarily incomplete. In addition to the ten behavioral items analysed and interpreted, items concerning water use, i.e. wetting of the ventral plumage on a water surface, behavior under the rain, etc. must be added.

It is likely that other behaviors will be observed and recorded in other places and circumstances which will enhance this dataset. Comparison of the data between the two years shows that already in 2017, almost all the ten grooming behaviors had been recorded in the Common Swift. However, the 2018 records made it possible to enhance the database and improve the validity of calculations concerning the average durations and frequencies of various behaviors.

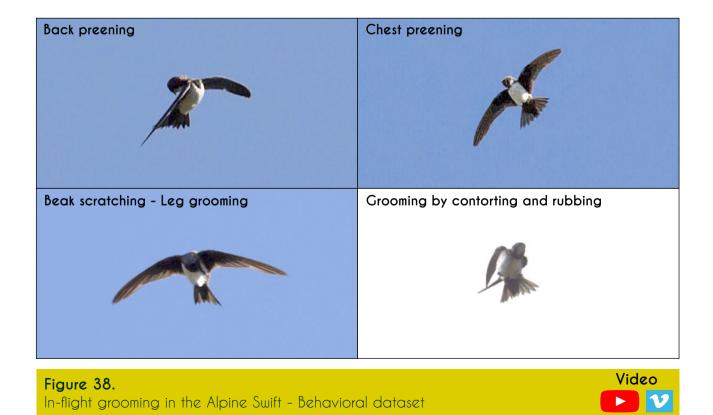
In comparison, the **Figure 38** also shows a first behavioral dataset of in-flight grooming in the Alpine Swift.

Let's start with a surprising remark. For

the Common Swift, I spent 65 days of observations with four hours per day shooting on average that is a total of 260 hours. In contrast, for the Alpine Swift, the videos were recorded over a very short period of time. Indeed, during two mornings, the birds came only for a few minutes flying over my head to forage!

Yet, four of the behaviors studied in the Common Swift have been identified in the Alpine Swift, not to mention the capture scenes that will be analyzed in a second paper.

The comparative study of the in-flight grooming of these two species revealed very strong similarities in the postures used as well as in their average durations. Bird morphologies that differ only in size and same constraints related to the very long flight times result in very similar grooming behaviors.



In flight behaviors in Common Swift - Grooming Jean-François CORNUET 102

7. In-flight grooming in birds

In an flying bird, any activity that may displace the plumage can cause wholebody shaking to put again feathers in good order (GOODWIN, 1959). For example, this behavior is observed in birds that fish from flying and diving into the water. Rapid shaking and twisting of the body and wings eliminate some of the water from the plumage (Terns, Osprey, etc.). When diving is a bath to clean the plumage, the bird also continues its flight by shaking its plumage (Terns, Swifts, Swallows, Beeeaters, Orioles,...).

Similarly, when a bird is released after handling for a ringing operation, it is common for many species to shake themselves after taking off.

Shaking the plumage in flight is therefore the most common and widespread behavior in birds. Because it is a fast movement that does not require special attention, it is not necessarily limited to birds with unusual flying abilities.

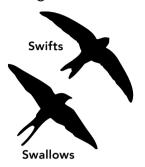
The Common Swift is therefore not the only bird capable of grooming in flight.

From my shots (photos and videos) and my research on the Web, I constructed a table (**Table 5**) of bird species able for in-flight grooming. Many species will be added to this Table over time. However, when reading this ranking, 4 main groups of species seem to show definite abilities for this type of behavior. It should be mentioned, however, that many species are difficult to photograph and film in flight.

7.1. The 4 main groups of birds able to groom themselves regularly in fligh

Swifts and Swallows

These species have in common a short, triangular and flat bill, a wide gape, small



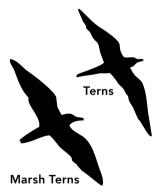
legs and very long wings relative to their size (wingspan: 30 to 45 cm).

They feed exclusively on insects caught in flight. Swallows spend a large part of

their daytime in aerial hunting; Swifts lands only for breeding. Alternating gliding and flapping flights, they are birds with great aerial capacities, capable of acrobatic manoeuvres, sudden changes in trajectory...

Terns and Marsh Terns

These medium-sized waterbirds have in common a thin, pointed bill, small legs, long, tapered wings (wingspan 55 to 135 cm) and an often indented tail. Their silhouette and elegant flight deserved them the name of Sea swallows. Closely lin-



ked to the water, they catch small fish by diving or they catch insects on the surface of water. Terns and MarshTerns, alternating gliding and flapping flight, are capable of acroba-

tic manoeuvres and sudden changes in trajectory. They spend most of their lives in the air, whether for foraging, travelling or long-distance migrating.

Table 5. List of bird species photographed or filmed grooming in flight

				(Grooming with the beak]						
Orders	Families	Species	Wingspan cm	Back	Tail feathers	Chest Belly	Legs	Head scratching	Contorting and rubbing	Wings fluttering	Roll	Head rotation closed beak	Head rotation open beak
Apodiformes	Apodidae	Common Swift (Apus apus)	42-48			٠			•	•	٠	•	•
Apodiformes	Apodidae	Alpine Swift (Tachymarptis melba)	54-60			٠			•				
Apodiformes	Apodidae	Chimney Swift (Chaetura pelagica)	30					w					
Apodiformes	Apodidae	Little Swift (Apus affinis)	33	w									
Passériformes	Hirundinidae	Sand Martin (Riparia riparia)	26-29			G				•		•	
Passériformes	Hirundinidae	Eurasian Crag Martin (Ptyonoprogne rupestris)	32-35										
Passériformes	Hirundinidae	Purple Martin (Progne subis)	40			G		B					
Passériformes	Hirundinidae	Grey-breasted Martin (Progne chalibea)	??					B					
Passériformes	Hirundinidae	Tree Swallow (Tachycineta bicolore)	30-35					B					
Passériformes	Hirundinidae	White-winged Swallow (Tachycineta albiventer)	??					B					
Passériformes	Hirundinidae	Rough-winged Swallow (Stelgidopteryx serripennis)	??					B					
Passériformes	Hirundinidae	Barn Swallow (Hirundo rustica)	32-35					w G				•	
Passériformes	Hirundinidae	Red-rumped Swallow (Cecropis daurica)	32-34					w					
Passériformes	Hirundinidae	Common House Martin (Delichon urbicum)	26-29			w		w					
Ansériformes	Anatidae	Gadwall (Mareca strepera)	84-95										
Falconiformes	Falconidae	Eurasian Hobby (Falco subbuteo)	68-84										
Accipitriformes	Accipitridae	Western Marsh Harrier (Circus aeruginosus)	110-130						•				
Ciconiiformes	Ciconiidae	White Stork (Ciconia ciconia)	155-165			w							
Pelecaniformes	Pelecanidae	Brown Pelican (Pelecanus occidentalis)	200-230					w					
Pelecaniformes	Threskiornithidae	American White Ibis (Eudocimus albus)	97	w		w							
Suliformes	Sulidae	Northern Gannet (Morus bassanus)	165-180			w		w					
Suliformes	Sulidae	Masked Booby (Sula dactylatra)	150-170			w							
Suliformes	Fregatidae	Ascension Frigatebird (Fregata aquila)	200			w		8					
Suliformes	Fregatidae	Magnificent Frigatebird (Fregata magnificens)	215-245			w		ß					
Suliformes	Fregatidae	Great Frigatebird (Fregata minor)	205-230			w		ß					
Suliformes	Phalacrocoracidae	Great Cormorant (Phalacrocorax carbo)	130-160			w							
Suliformes	Laridae	European Herring Gull (Larus argenteus)	135-145					G					
Charadriiformes	Laridae	Western Gull (Larus occidentalis)	132-142			G		G					
Charadriiformes	Laridae	Glaucous-winged Gull (Larus glaucescens)	132-137			-		G					
Charadriiformes	Laridae	Ring-billed Gull (Larus delawarensis)	121-127			w		G					
Charadriiformes	Laridae	California Gull (Larus californicus)	122-140			w		-					
Charadriiformes	Laridae	Black-headed Gull (Chroicocephalus ridibundus)	94-110			w							
Charadriiformes	Laridae	Black-legged Kittiwake (Rissa tridactyla)	91-97	w		w							
Charadriiformes	Laridae	Black Skimmer (Rynchops niger)	107-127			w							
Charadriiformes	Laridae	Black Tern (Chlidonias niger)	57-65	G		G		G					
Charadriiformes	Laridae	White-winged Tern (Chlidonias leucopterus)	58-67	Ľ				w					
Charadriiformes	Laridae	Sooty Tern (Onychoprion fuscatus)	82-94					G					
Charadriiformes	Laridae	Common Tern (Sterna hirundo)	72-83										
Charadriiformes	Laridae	Bridled Tern (Onychoprion anaethetus)	72-83	-			-	w					
Charadriiformes	Laridae	Royal Tern (Thalasseus maximus)	100-135	-			-	w					
Procellariiformes	Diomedeidae	Light-mantled Albatross (Phoebetria palpebrata)	183-232	-		G		G					
Procellariiformes	Diomedeidae	3					-	G					
		Wandering Albatross (Diomedea exulans)	254-351	-			<u> </u>	G					
Procellariiformes Procellariiformes	Diomedeidae	Southern Royal Albatross (Diomedea epomophora)	305-351	-		w	<u> </u>	9					
riocellamiormes	Diomedeidae	Shy Albatross (Thalassarche cauta)	272-354			•••							

Personal videos and photographs

w Photographs found on the Web

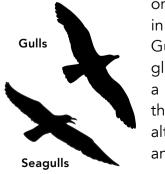
G Published observational data (Goodwin, 1959)

K Published observational data (Kramer, 1964)

B Published observational data (Burtt, 1988)

Gulls and Seagulls

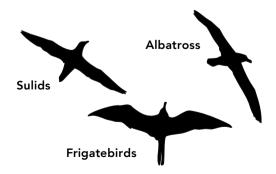
These waterbirds are more robust than terns, with wider wings (wingspan 120 to 150 cm) and longer legs. Whenever



on coasts, at sea or in inland wetlands, Gulls are excellent gliders that spend a large part of their lives in the air, alternating flapping and gliding flight.

Sulids, Frigatebirds and Albatross

With their long and narrow wings (wingspan 150 to 350 cm) these seabirds perfectly master gliding over seas and oceans.



These four groups spend most of their time on the wing, hunting aerial prey (Swallows and Swifts), or aquatic prey caught by diving (Terns, Sulids,...) or are sea surface (Gulls, Frigatebirds and Albatrosses).

Travelling long distances daily, they have excellent gliding skills with long, tapered wings.

These morphological and behavioral traits allow these birds to spend some time groooming while on the wing.

If the bird loses some altitude during in-flight grooming, an upward flight may precede the behavior: this bell shaped flight has been shown in the Common Swift (PICHOT, 2017), Black Tern (GOODWIN, 1959), and Common Tern.

7.2. The two most observed behaviors

1. In-flight head and neck scratching with a leg

In **Table 5.**, 31 species (70%) were observed performing this behavior in flight.

Pictures and observations (GOODWIN, 1959 ; KRAMER, 1964 ; BURTT, 1988) show that, in flight, head-scratching is always performed by the direct method (the leg passing under the wing).

We had already pointed out the particular behavior of swallows (Burtt, 1988) and frigatebirds (KRAMER, 1964), which use:

- the direct method (the leg passing under the wing) when scratching in flight;
- the indirect method (the leg passing over the wing) when scratching, while sitting or perched.

Remember that the Common Swift uses the direct method in flight, and either method when settling down in the nest.

This difference has been related to changes in the position of the gravity center relative to the locomotor system, depending on whether the bird is perched or in flight (Goodwin, 1959).

Except in the Gadwall, which scratches while in flapping flight, this grooming behavior is always practiced during a gliding flight, which facilitates the maintenance of the bird's balance and and provides a good perception of its environment.

2.2. Grooming the underside (chest, belly, axilliaries, wing underside) with the bill

Nearly 22 species (50 %) have been observed using this behavior in flight.

Depending on the length of the neck and bill, accessible areas of the body are more or less distant from the head. With a very short neck and bill, the Common Swift and Swallows are limited for grooming the chest, axillaries and underside of wings basis. In contrast, with its long neck and ca 18 cm long bill, the White Stork can reach the entire underside of the wings.

It is not surprising that these two kinds of grooming are the most frequently observed.

Concerning the Common swift, we already noted that head scratching and chest grooming are behaviors with the lowest altitude loss and the best preservation of the environment perception.

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Conclusion

Slow motion video appears as the modern form of chronophotography, as it was named in 1889 by **Étienne-Jules Marey**. According to Wikipédia: **Chronophotography** is defined as "a set of photographs of a moving

object, taken for the purpose of recording and exhibiting successive phases of motion".

In 1968, OEHME used this technique with a camera filming at a rate of 80 fps based on the captions in the illustrations of his papers on the flight of the Common Swift.

In 1973, G. ET H. ROTHGÄNGER also used photographs.

Today, hybrid digital cameras, which can film at high frame rates, are a good tool to deepen the study of fast movements in animals.

The study I conducted on the in-flight behaviors of the Common Swift does not require significant technical resources. Swifts are still common birds in cities, although building renovation makes it more and more difficult for them to find nesting cavities. They pass and pass again over our heads hundreds of times. The biggest challenge is to keep them sharp in the viewfinder for a few seconds...

Comparative studies have shown that many species are able to display a high diversity of flight behaviors that have been little studied so far.

I hope that this work will provide ideas for similar work to enhance the behavioral datasets from visual observation.

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, reverse flight, duo-flight...



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