Frigate birds track atmospheric conditions over months-long transoceanic flights and perform flights inside clouds

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Abstract

Understanding how animals respond to atmospheric conditions across space is critical for understanding the evolution of flight strategies and long-distance migrations. We studied the three-dimensional movements and energetics of great frigate birds (Fregata minor) and showed that they can stay aloft for months during transoceanic flights. To do this, birds track the edge of the doldrums to take advantage of favorable winds and strong convection. Locally, they use a roller-coaster flight, relying on thermals and wind to soar within a 50- to 600-meter altitude band under cumulus clouds and then glide over kilometers at low energy costs. To deal with the local scarcity of clouds and gain longer gliding distances, birds regularly soar inside cumulus clouds to use their strong updraft, and they can reach altitudes of 4000 meters, where freezing conditions occur.

Introduction

The movement of animals is driven by processes that act across multiple spatial and temporal scales. Long-distance movements such as the migrations of birds have evolved in response to large-scale environmental gradients [1]. In particular, atmospheric conditions play a large role in determining the efficiency of migratory routes, whose consistency over years has allowed evolutionary processes to act at population levels [2]. At smaller time and spatial scales, long range movements have to constantly be adjusted to local conditions, in particular to minimize energy expenditure [3, 4]. These long movements or migrations can be done over inhospitable areas as different as deserts, high mountains or oceans, which come with specific environmental constraints to which birds need to behaviorally and physiologically adapt their flight strategies [5, 6]. How these long restless flights can be energetically achieved has attracted much interest, but remains largely unknown because of the inherent difficulties of studying such behaviors in situ.

Biologists have long been attracted to locomotor extremes because they provide clear examples from which information about structure-function relationships can be drawn [7]. Among birds, frigate birds are extreme in many aspects of their life history, including having the lowest wing loading, with a specialized capacity for soaring flight [8]. They are also unusual seabirds because their feathers are not waterproof and their legs are small, so they are unable to land on the sea surface even though they feed exclusively at sea. They deal with these conflicting constraints by staying aloft for days when they are foraging from their nest when breeding [9]. Probably as a consequence of these extreme attributes, frigate birds have the longest period of parental care in birds, suggesting a long period of learning to acquire flight and foraging abilities in early life [10]. Their ability to remain airborne continuously for days is probably possible because of the capability of frigate birds to use thermals over the sea as a main energy source for soaring [11, 12].

We asked how frigate birds can perform long migrations over oceans without landing and whether oceanic thermals are reliable enough in space and time to allow birds to stay airborne over long periods. To address these questions, we investigated the movement of frigate birds at several spatial scales with regard to

(i) how frigate birds make use of large-scale weather systems to perform long-range movements, and

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(ii) how flight dynamics and energetics at a finer scale contribute to these long ranges.

Transoceanic flights of frigate birds

We studied the three-dimensional movements and energetics of frigate birds on Europa Island (Fig. 1) between 2011 and 2015 [13]. To study large scale migratory movements, 24 adults and 25 juvenile birds were equipped with solar-powered Argos transmitters [13]. To study the relationship between heart rate, activity (flapping frequency), and behavior (ascent rates and horizontal speed), 11 adult females were equipped with external custom-designed loggers measuring triaxial acceleration and electrocardiography and a Global Positioning System (GPS) device [13]. To study movements, activity, and ambient temperature, 37 adult females and males were equipped with solar powered GPS accelerometers, whose data were recovered regularly by an automatic recording station [13].

During the southwest Indian monsoon from June to October, strong trade winds occur in the southern Indian Ocean and cross the equator to form southwest winds in the northern Indian Ocean [14] (Fig. 1). During this season, adult frigate birds finishing the breeding season left Europa and migrated northward to take advantage of the southerly winds. They settled on roosting sites in the Seychelles from where they foraged for months. Some adults performed long looping movements around the equator, where a belt of converging air and wind occurs, with no wind in the center, named the doldrums zone by ancient mariners (Fig. 1). On successive loops, adults closely followed the edges of the doldrums, which oscillate longitudinally (Fig. 1, A and B). Birds stayed continuously on the wing for periods lasting up to 48 days and traveled on average 420 ± 220 km daily.

Young frigate birds left their birthplace at the same time as adults, but independently of their parents. They crossed the equator and turned eastward to enter into a circular transoceanic movement into the wind belt around the doldrums (Fig. 1, C and D). During these dispersive movements, juvenile birds stayed continuously aloft for flights lasting up to 2.1 months (average maximum time spent aloft, 41.2 ± 15.1 days, n = 8 birds). They travelled on average 450 ± 220 km daily. They episodically stopped on isolated islands such as Chagos, islets off Indonesia, or on islets of the Seychelles archipelago for very short rests (8 hrs to 48 hrs) before continuing their large-scale wandering movement tracking the edge of the doldrums (Fig. 1C). They flew at altitudes ranging between the sea surface and 3000 m, but mainly between 0 and 600 m.

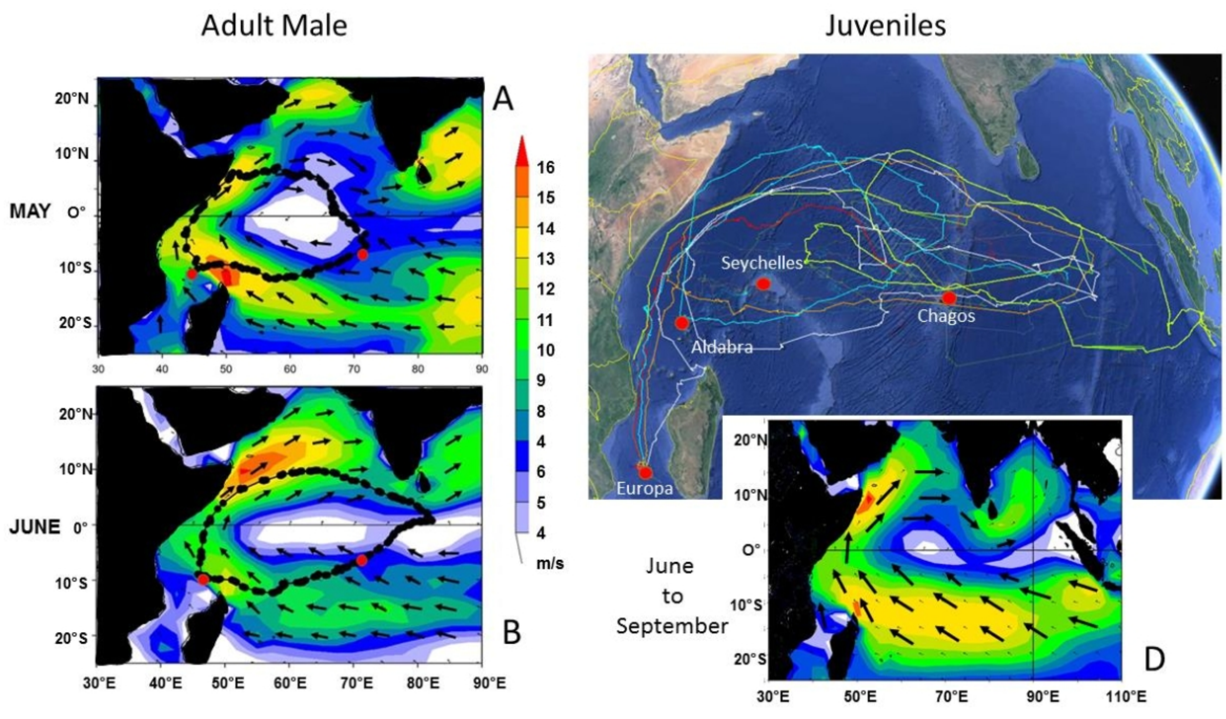

Fig. 1: Movements of adult and juvenile frigate birds in relation to wind conditions in the Indian Ocean.
(Left) Two successive clockwise movements from Aldabra Island (Seychelles) of an adult male great frigate bird (no. 138502) in relation to wind strength (in meters per second, color scale) and direction (arrows). (A) In May 2015, a 24-day foraging trip around the doldrums (shown by the absence of wind, in white),with 1 day of rest in Chagos. (B) In June 2015, a28-day foraging trip,with a 36-hour rest in Chagos. (C) Movements between June and September 2015 of six young frigate birds fledged from Europa Island, moving around the doldrums zone. (D) Climatology of wind speed and direction (average values over 4 months) in June to September 2015, showing the average position of the doldrums (white) on the equator.

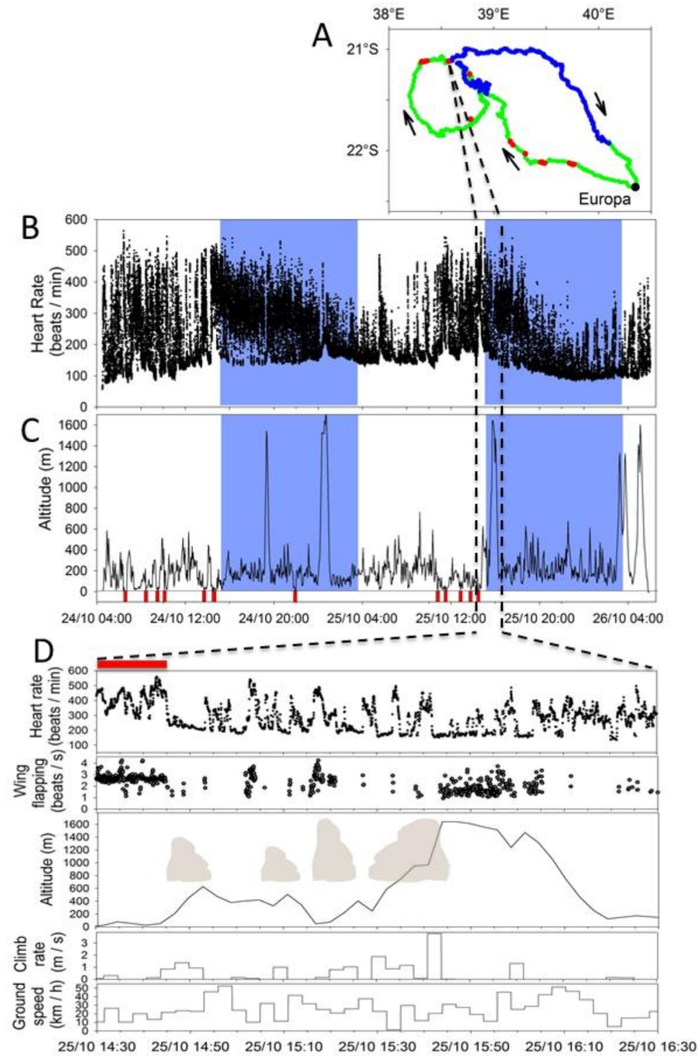

Fig. 2: Movement, changes in altitude, heart rate, and flight parameters during a 2-day trip at sea.

(A) 1130-km-long movement from Europa during the daytime (green) and night (blue) with foraging bouts in red, with recorded (B) heart rate and (C) altitude. Shaded blue areas represent nighttime, and red blocks represent foraging bouts. (D) A 2-hour period during the trip at sea, with an active foraging phase followed by a traveling phase, showing the changes in altitude and corresponding heart rate, wing flapping rate, climb rate, and ground speed. On the altitude panel, the predicted presence of cumulus clouds is indicated (gray).

To understand how frigate birds are able to stay aloft for such long periods, we studied their flight dynamics and energetics during 2- to 15-day foraging trips from Europa. Breeding frigate birds travelled on average 410 $\pm$ 142 km per day (n=18 birds), mainly during the daytime, traveling over shorter distances at night (Fig. 2). Two clear behavioral modes were identified during movements at sea. Traveling occurred with high ground speeds and low wing beat frequencies (82 $\pm$ 9% of travelling time with no or rare wing beats),with birds remaining at altitudes ranging from 30 m to 2000 m, reaching up to 4120 m. Foraging can only occur when birds descend close to the sea surface (altitudes 0 to 30 m), and during these periods they are very active, flapping during 75 $\pm$ 18% of the foraging phase (Fig. 2). Active foraging occurred only episodically (10 $\pm$ 7% of time at sea), indicating rare feeding opportunities, mainly during the day (86.4% of bouts of active foraging occurred during the daytime).

When in flight at sea, heart rate was on average 203 $\pm$ 84 beats min^{-1} but varied extensively (Fig. 2), occasionally attaining values as low as when resting on the nest (71 $\pm$ 25 beats min^{-1}, range 57 to 215). Heart rate and dynamic body acceleration were generally well correlated [13]; therefore, we used dynamic body acceleration, measured on all individuals, as the main proxy for energy expenditure. Whereas active foraging is very costly for frigate birds, requiring high dynamic body acceleration and heart rates, traveling periods have a remarkably low energy expenditure, with few wing beats (Fig. 2), suggesting that overall field metabolic rate during months at sea is likely to be exceptionally low [13]. Excluding periods of active foraging close to the surface, dynamic body acceleration was the lowest at altitudes between 300 and 600 m, indicating an optimal altitude for traveling at low cost.

Traveling at low cost is achieved by successive climbs,mainly through soaring with no or few wing flaps and low heart rate, and descents, by gliding (Figs. 2 and 3). A close examination of flight paths shows that when soaring, birds move with the wind, using circling movements to soar (Fig. 3C) in thermals below cumulus clouds where rising air creates updrafts [15]. Because of the strong trade winds, they drift with the wind while climbing (Fig. 3), resulting in wind-drift circling soaring. Conversely, when gliding, they preferentially fly with side winds and achieve the highest ground speeds (Figs. 2 and 3). The resulting movement is a complex zig-zagging, roller-coaster movement, with an average altitude gain of 59.1 $\pm$ 43.8 m per kilometer covered (ground distance); i.e., 15.4 $\pm$ 3.0 km climbed daily. These vertical movements take place generally up to 600 m to 700 m, corresponding to the base of the cumulus clouds that is relatively constant throughout the trade wind zone [16].

However, birds regularly climbed up to altitudes higher than 700 m. Climbing to high altitudes can be separated into a phase of slow climb up to the base of the cumulus clouds at 600 m to 700 m, followed by a more rapid climb to 1600 m (Fig. 2D) or higher. This second phase of the ascent is performed without flapping the wings (Fig. 2D); i.e., in pure soaring flight. Ascent to high altitude can only take place inside cumulus clouds, where updrafts reach 5 m/s and are strong enough to provide large climb rates [15]. During the gliding phase made outside the clouds, the minimum sink rate was 23.6 $\pm$ 19.1 m of ground distance covered per meter lost between 500 m to 700 m altitudes, compared to 14.3 $\pm$ 11.7 m at higher altitudes ($F_{1,7}$ = 8.4, P = 0.045).

Our study shows that frigate birds can remain almost indefinitely on the wing by tracking, at a basin-wide scale, the wind

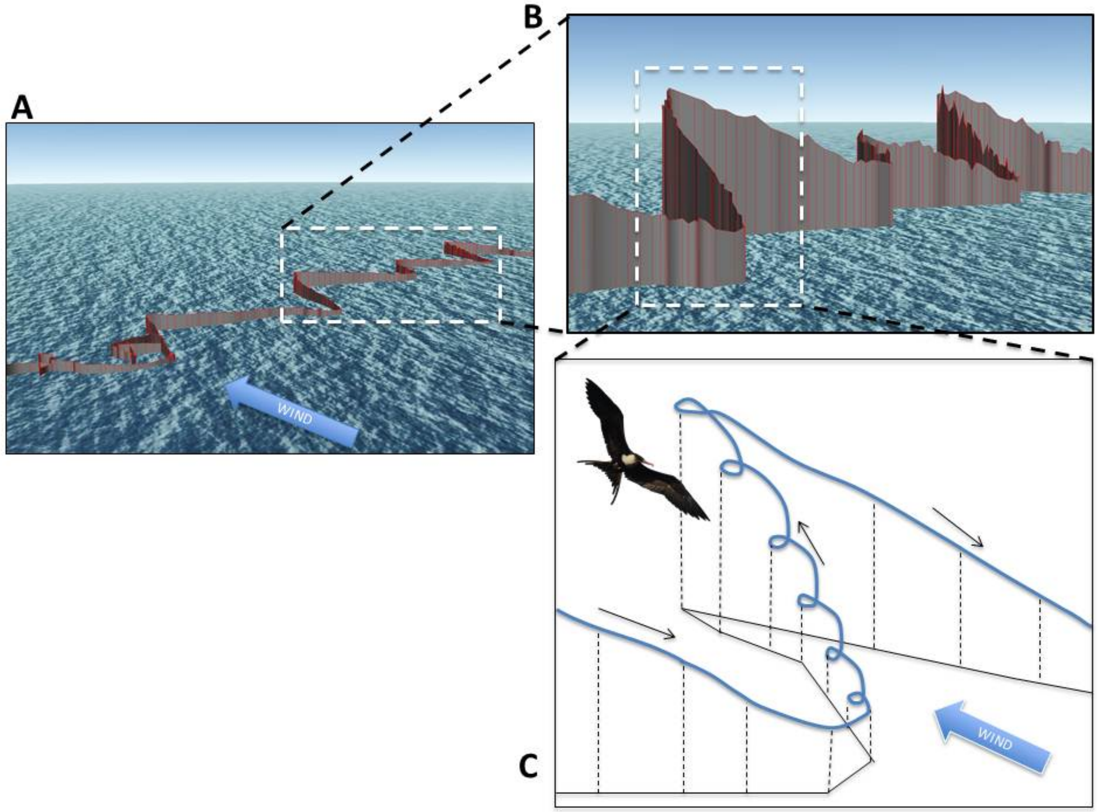

Fig. 3: Three-dimensional movement of a frigate bird at three scales.
(A) Section of a track of a frigate bird traveling with side winds. (B) Enlargement showing the movement alternating gliding and soaring, resulting in a zig-zag and roller-coaster movement. (C) Detailed schematic representation of a single cycle of soaring and gliding, illustrating the climb by circling, with a resulting drift due to wind, followed by the descent.

belt around the doldrums, an atmospheric feature whose location is predictable. Locally, they display a specific flight strategy based on an energy-efficient use of convection and wind. By using wind-drift circling soaring and long periods of gliding, frigate birds are able to simultaneously use convection and wind as energy sources and move over extensive distances at low energy costs. They favor altitudes between 50 m and 600 m, where atmospheric conditions are optimal for low-cost flight; i.e., steady winds and updrafts from convection under clouds (Fig. 4). These altitudes are also convenient to spot feeding opportunities from long distances away during the daytime; birds then descend close to the surface to forage actively when feeding opportunities have been detected [9].

Although birds are not thought to carry out intentional, sustained cloud climbs [17, 18], our study shows the ability of frigate birds to frequently ascend to very high altitudes inside clouds. At an altitude of 4000 m, air temperatures are negative and air density and oxygen availability are almost half of those at sea level [17], suggesting that this tropical bird encounters extreme conditions at such altitudes. Cumulus clouds and cloud fields are considered to be randomly distributed in space in the trade wind zone [16]. In these conditions, climbing higher than 1000 m presents a fundamental advantage by allowing frigate birds to cover much longer distances by gliding to reach the next updraft under clouds. Therefore, when clouds are sparsely distributed, birds can adjust their gliding distance by climbing higher to avoid the risk of switching to costly flapping flight. Juvenile individuals are able to master the flight strategy of adults as soon as they become independent. When they leave their birthplace, they all head north to reach the equator and circle the entire Indian Ocean. This stereotyped movement suggests a genetically encoded behavior that brings young individuals directly to a predictable, favorable, and large-scale atmospheric feature located thousands of kilometers from their birthplace.

Great frigate birds are the only birds other than swifts [19] to be able to stay aloft for months. Long periods in continuous flight are interrupted by very short periods of rest on land, suggesting that frigate birds might sleep while airborne [20]. Periods of low activity (no flapping) occur mainly during soaring episodes and may allow sleep. However, periods of completely motionless (no flapping at all) flight, potentially corresponding to periods of sleep, are relatively short, (2 min, never exceeding

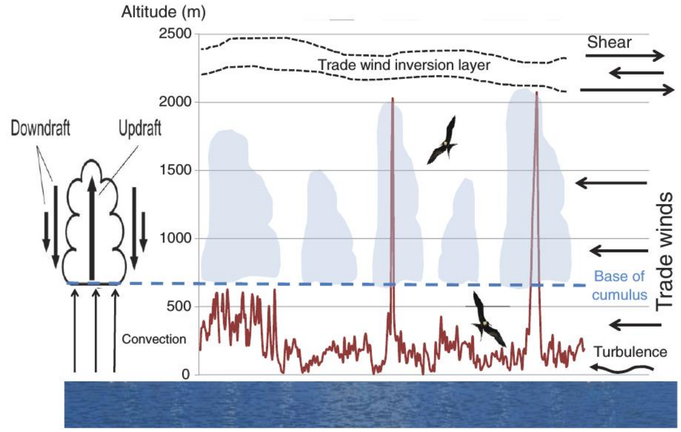

Fig. 4: Altitudinal movement of a frigate bird in relation to potential atmospheric conditions.
The traveling flight is performed between 30 and 600 to 700 m altitude in a band with regular winds, avoiding the turbulence close to the surface. The bird occasionally climbs to 2000 m within cumulus clouds that form by convection, whose base is at 600 to 700 m and whose vertical extension is limited by the inversion layer where strong shear occurs. A schematic presentation of the updrafts and down drafts characteristic of cumulus clouds is shown at left [24]

12 min). Animals such as frigate birds may have evolved the ability to dispense with sleep when ecological demands favor wakefulness such as during extended flights [21], but studies are needed to determine how they sleep during much longer-lasting flights.

Frigate birds clearly encounter several atmospheric challenges during their movements at sea, such as low temperatures, low air density and oxygen levels during high climbs, and the unpredictable distribution of cumulus clouds at small scale, together with the presence of powerful cyclones in their optimal range. This dependence on atmospheric systems could make them particularly sensitive to future climate changes, along with some other seabirds [22]. Climate models for the tropical ocean forecast an increase in the intensity of tropical storms and of convections around the equator, where the doldrums and strong convections occur [23]. More variable atmospheric conditions in the future may become too challenging for a species that already seems to encounter extreme conditions during its lifetime movements.

Flights of frigate birds inside clouds

The unique ability of frigate birds to fly inside clouds raises questions about the mechanical energy balance, possible energy advantages or the control of flight. Such questions are of great interest with regard to soaring and gliding in general, including application to piloted sailplanes. Some of those aspects will be dealt with in the following treatment.

An issue is whether or not frigate birds are able to perform regularly flights inside clouds. Exemplary results are presented in Fig. 5 where a number of flights inside trade cumulus clouds are shown. The maximum altitude achieved in each of the flights inside a cloud is well above the cloud base the altitude of which is about 600 m to 700 m in the trade wind zones [25]. There is one flight where an altitude higher than 4000 m was reached. Furthermore, the bird performs flights inside clouds during daytime as well as at night. The results presented in Fig. 5 suggest that frigate birds intentionally and regularly perform flights inside clouds.

Ascending flights inside clouds to high altitudes such as 4000 m is a unique ability of frigate birds when compared with all other seabirds. That ability provides an unparalleled possibility to cover large distances at little or even no mechanical energy cost. This is graphically addressed in Fig. 6 where flight scenarios for covering the distance between two trade cumulus clouds 80 km away from each other are shown. Two flight modes denoted by 1 and 2 are considered. For both flight modes, the maximum distance achievable in gliding flight plays an essential role. The maximum gliding distance is generally given by the relation [26]

$$x_{max} = (L/D)_{max} \cdot h,$$

where $(L/D)_{max}$ is the maximum lift-to-drag ratio of the bird and h is the altitude at the beginning of the glide. For the problem under consideration, it is assumed that

$$(L/D)_{max} = 20.$$

Flight mode 1 which is graphically addressed in the upper part of Fig. 6 applies to the altitude region below cumulus clouds where the bird climbs by circling soaring in an updraft until the cloud base at h = 600 m is reached. From that altitude, the bird can glide over a track length of x_{max} = 12 km at no mechanical energy cost. Subsequently, the bird can no longer climb by soaring in rising air as there are no more updrafts available. Thus, the bird has to perform a flight involving continuous flapping for

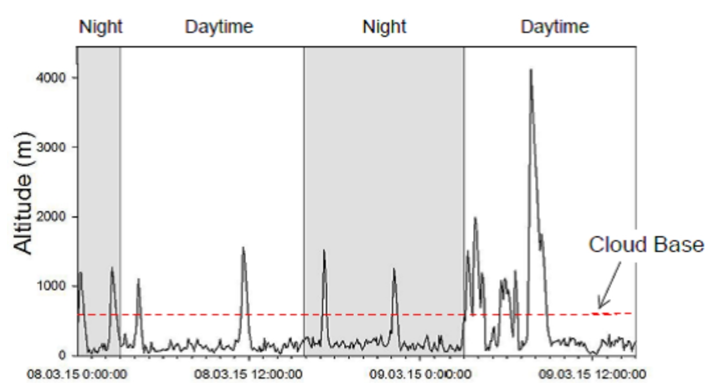

Fig. 5: Flight inside clouds during daytime and night.
The altitude profile recorded during a 2.5-day foraging movement of a frigate bird is presented. There are ascending flights inside clouds at daytime as well as at night, showing altitudes at top of climbs well beyond the cloud base. The highest altitude reached is 4120 m.

the remaining 68 km to the adjacent cumulus cloud. As a result, there is a correspondingly large mechanical energy cost for the major part of the distance between the two clouds.

Flight mode 2 which is graphically addressed in the lower part of Fig. 6 shows an ascending flight inside the first cloud using an updraft for circling soaring up to h = 4000 m and a subsequent glide. From h = 4000 m, the bird glides over a track length of x_{max} = 80 km, thus covering the 80 km to the next cumulus cloud in gliding flight, without any flapping. In this scenario, birds

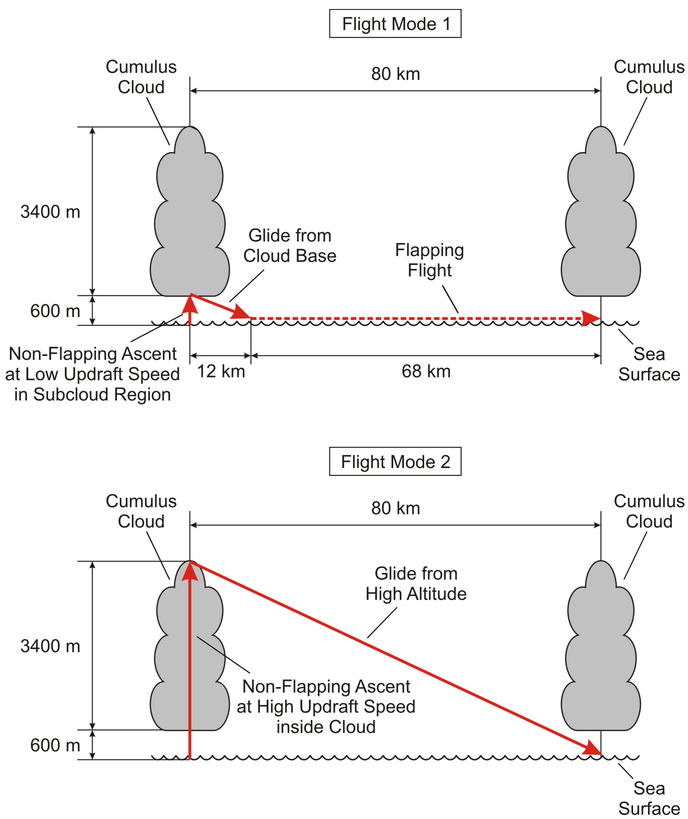

Fig. 6: Distances achievable in glides following ascent below the cloud base and an ascent inside a cloud.

Flight mode 1 is made up of 3 sections. The first section is a circling ascent in an updraft in the altitude region below the cumulus cloud base. In the second section, the bird glides from the cloud base to the sea surface over a ground distance of 12 km. The third section consists of a horizontal flight using flapping until the next cumulus cloud is reached. The remaining distance to reach the adjacent cumulus cloud by means of flapping flight is much longer than the distance covered in gliding flight.

Flight mode 2 comprises 2 sections. The first section is a circling ascent in an updraft inside the cumulus cloud. In the present case a high altitude of 4000 m is supposed to be reached, corresponding with measurement results presented in Fig. 1. The second section shows a glide from the highest altitude to the sea surface. The track distance achieved in gliding flight is 80 km which means the whole distance between the two clouds is covered in gliding flight so that there is no mechanical energy cost.

can travel the entire distance between the two clouds without a mechanical energy cost. As a result, the possibility of flying inside cumulus clouds to increase the achievable altitude yields a considerable energy advantage compared with flight mode 1.

Flight mode 2 is an issue in the case of widely spaced clouds. Oceanic trade cumuli involve irregular groups or clusters of about 10 km to 50 km across and separated by somewhat wider clear areas [27]. Thus, there can be large differences in the distances between clouds which a frigate bird has to cover when flying from one cloud (or cloud group) to the other. This means that flight mode 2 yields a significant energetic advantage for the travelling of frigate birds.

How frigate birds manage to control and perform flights inside clouds is of great interest. For dealing with that aspect, a closer look at flights inside clouds is provided in Fig. 7 which shows — on a small-scale basis — the altitude profile of ascents of a frigate bird inside a trade cumulus cloud and below the cloud. Climb rates in ascents below the clouds are around 0.5 m/s. That is a relatively small climb rate which corresponds with the low updraft speeds existing in the altitude region below trade cumulus clouds [27]. By contrast, the climb performance of flights inside the cumulus cloud is higher. In Fig. 7, a climb rate of 3.3 m/s was achieved by the bird, a 6-fold increase compared with a 0.5 m/s climb rate below the cloud. The large climb rate is due to the high updraft speed existing inside the cumulus cloud. The fact that such high updraft speeds are possible in trade cumulus cloud has been confirmed by direct measurement [15].

Furthermore, the results presented in Fig. 7 show that the ascents are of consistent and steady nature. This suggests that the bird is capable of performing such flights in a controlled and stabilized manner which would allow them to conduct the flights inside clouds regularly and consistently.

The fact that frigate birds have the ability to fly inside clouds is all the more noteworthy, as there are severe and adverse environmental conditions. One of those conditions is the lack of visibility in clouds, with no visual cues for an orientation in space. In aircraft, gyroscopic type instruments provide the required information for spatial orientation in clouds. However, no biological sense organ providing analogous information is known in birds [17]. Accordingly, it is assumed that sustained, controlled flight in clouds is not possible for birds [17, 18, 28, 29]. Further to demanding environmental conditions, the air inside trade cumulus clouds shows increased turbulence levels [15]. Turbulence means that birds are exposed to effects disturbing their motion, potentially leading to deviations from the desired flight path. The disturbing effects are stronger with a higher turbulence level. Combined effects of lack of visibility and high turbulence can result in an even more demanding environmental condition.

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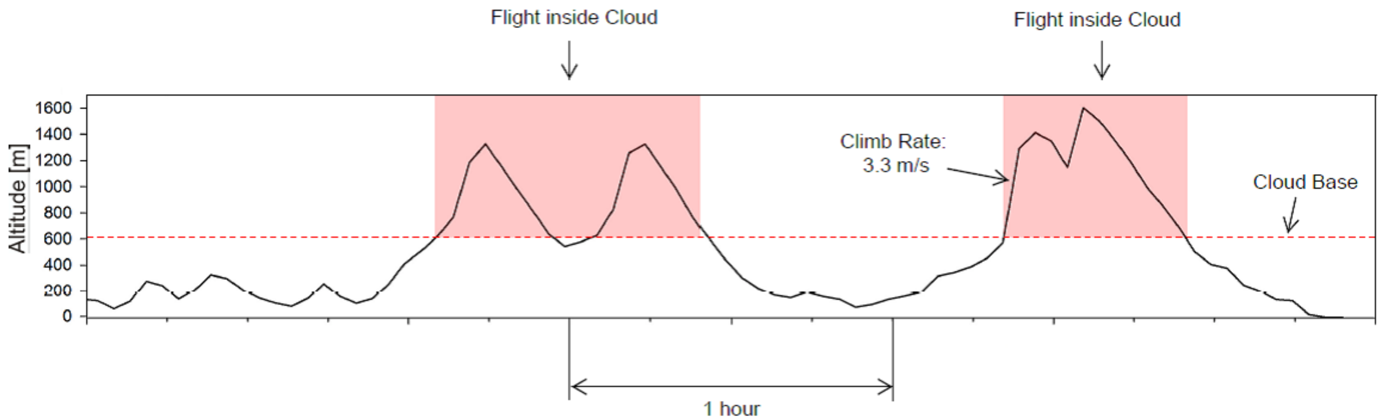

Fig. 7: Climb performance achieved with ascending flights inside cloud and below cloud.
The altitude profile recorded during the flight of a frigate bird below and inside clouds is shown on a small-scale basis. The climb rate achieved in the altitude region below the cloud base is around 0.5 m/s, while climb rates of a bird ascending inside a cumulus cloud can be much higher. In the presented case, a climb rate of 3.3 m/s was achieved.

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