Flight of frigatebirds inside clouds – energy gain, stability and control

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**Abstract**

Investigating the unique ability of frigatebirds of flying inside clouds, it is shown that they achieve a large energy gain by ascents to high altitudes in strong updrafts of trade cumulus clouds. Frigatebirds often perform that kind of flight, at daytime as well as in the night. This suggests that they are capable of flying inside clouds in a controlled and stabilized manner. The control requirements for ascents in terms of a circling flight in updrafts of trade cumulus clouds are analyzed, and the necessary aerodynamic control moments are determined. Based on a stability investigation, it is shown that there are restoring effects which act against disturbances causing possible deviations from the circling flight condition. The aerodynamic moments which effectuate that stabilization are identified. Furthermore, the problem of neutral azimuth stability which generally exists in the flight of birds and which is the reason for continually increasing deviations from the course is dealt with. It is shown for the circling flight mode of frigatebirds inside clouds that, here, deviations are small and remain constant, suggesting that a corrective control action is not required. This is particularly important for circling flight in conditions without a visual reference, like inside clouds.

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1. Introduction

Frigatebirds which live in the trade wind zones north and south of the Equator show a flight behavior that is very specific and distinct compared to other birds (Weimerskirch et al. 2003; Pennycuick, 1983). Though they feed exclusively at sea, frigatebirds are unable to alight on water or to swim (De Monte et al., 2012; Pennycuick, 2008). This way of living requires that the birds can remain aloft continuously day and night for extended periods of time without the need to land. Such an aerial life is possible because frigatebirds have flight mechanical and aerodynamic characteristics appropriate for that purpose (Pennycuick, 2008; Weimerskirch et al., 2016). This also relates to the fact that they can sleep in flight (Rattenborg et al., 2016). Further to the ability of an aerial life, frigatebirds can make use of meteorological conditions existing in their marine habitat that allow flight at minimum mechanical energy cost (Weimerskirch et al., 2003; Weimerskirch et al., 2016). Thus, the birds possess characteristics that provide them the ability to stay airborne for months and to travel thousands of kilometers at low costs (Weimerskirch et al., 2016).

The meteorological conditions of the trade wind zones yield an energy source in terms of updrafts associated with cumulus clouds that frigatebirds use to ascend in order to increase flight altitude and, thus, to attain a potential energy gain that enables a subsequent glide involving flying at no mechanical energy cost. Based on this energy gain, frigatebirds show two unique flight modes. One relates to the altitude region below trade cumulus clouds. The updrafts existing between sea-level and cloud base are comparatively weak (Malkus, 1954) so that flapping is partially required to support ascending (Weimerskirch et al., 2016). The other unique flight mode of frigatebirds which is subject of this paper relates to the altitude region inside trade cumulus clouds where strong updrafts exist (Malkus, 1958). Here, frigatebirds ascend without flapping to high altitudes so that there is no mechanical energy cost in achieving a correspondingly large potential energy gain (Weimerskirch et al., 2016). The ascent is followed by a glide outside the cloud which is also performed at no mechanical energy cost. As a result, there is zero mechanical energy cost of the entire flight cycle consisting of a non-flapping ascent and a glide. The question which is the focus of this paper is how it is possible for frigatebirds to perform regularly and safely sustained flights inside

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clouds and, notably, how such demanding flights can be controlled and stabilized since clouds are a difficult environment without visual cues and with disturbances due to high turbulence effects.

The addressed issue relates to the more general question of whether or not birds can perform sustained, controlled flights inside clouds. This is subject to a number of investigations (Pennycuick, 2008; Griffin, 1973; Able, 1982; Pennycuick, 1972; Alerstam, 1997; Dinevich and Leshem, 2010). There are different explanations and controversial findings and conclusions. Radar measurement devices were used to track birds (Griffin, 1973; Able, 1982). Observations suggested that birds were flying in or among clouds sufficiently opaque to impede greatly vision of the sky or the ground. Further to radar investigations, birds appeared to be flying within or between cloud layers, headings were random and tracks were slightly, but significantly less straight than when birds were flying beneath the clouds. Other observations were concerned with thermal soaring of birds (Pennycuick, 1972). These observations show that the birds enter cumulus clouds from the bottom, but probably do not climb far above cloudbase. There are also more recent papers addressing issues of flight in clouds (Pennycuick, 2008; Alerstam, 1997; Dinevich and Leshem, 2010). These investigations suggest that sustained, controlled flight in cloud is not possible for birds.

The purpose of this paper is to show that frigatebirds have the ability of flying inside clouds. The fact that they regularly perform this kind of flight, during daytime as well as nights, suggests that their flight inside clouds takes place in a controlled and stabilized manner. The stability and control characteristics of their flight inside clouds which consists of a non-flapping circling flight mode in strong updrafts of trade cumuli are analyzed. It is investigated which are the control requirements for this flight mode and which are the stability effects that generate restoring forces and moments. Furthermore, the problem of neutral azimuth stability that generally exists in the flight of birds and is reason for increasing deviations from a course is addressed. According to the results obtained for the circling flight mode of frigatebirds, possible deviations are small and do not increase. Since the birds stay well within an updraft if such deviations occur, no performance penalty results, implying that a corrective control action is not required. The findings presented in this paper suggest that frigatebirds show a unique controlled flight mode that enables them to perform sustained and stabilized flights inside clouds.

This paper is an extension of the research performed by the present authors and published in Weimerskirch et al. (2016) where for the first time results on the flight of frigatebird inside clouds were reported. In the current paper, we will examine in detail why frigatebirds – as the only bird known – have that capability of intentionally flying inside clouds and how this capability is based on their unique aerodynamic characteristics and size/mass properties.

2. Material and methods

The study was carried out on Europa Island (22.3° S, 40.3° E), in the Mozambique Channel in September-November (period of incubation and small chick brooding) 2011, 2012 and 2013 and in January-March (period of large chick rearing and fledging) 2014 and 2015. Adult brooding small chicks or feeding large chicks and juvenile birds were captured on or nearby the nests and were fitted with loggers recording Tri Axial accelerometer, GPS position and for some birds heart rates.

A total of 19 solar-powered GPS-accelerometer (GPS/ACC, e-obs GmbH, Munich, Germany) whose data are recovered regularly by an automatic recording station were deployed. The devices (130 x 30 x 12 mm, 30 g) were attached to the back feather with waterproof tape (Tesa, Germany). The weight of the transmitter was 1.88–3.55% of the frigatebirds weight. These devices were re-covered before the birds departure migration, maximum 5 months after the deployment. To study the relationship between heart rate, activity (flapping frequency) and behaviour (ascent rates, horizontal speed), 11 adult females were equipped with an external 18 g custom-built heart rate – accelerometer logger (Spivey and Bishop, 2014) and a GPS (i-gotU GT-120, Mobile Action Technology Inc., Taipei, Taiwan, 18 g). Birds were recaptured after one or several foraging trips at sea and the loggers recovered to download the data.

Details of analyses are given in Weimerskirch et al. (2016).

3. Results and discussion

3.1. Measurement results on flights of frigatebirds inside clouds

3.1.1. Updrafts in trade cumulus clouds and energy gain feasibility

Frigatebirds live in the trade wind zones which extend in areas north and south of the Equator. These zones show distinctive meteorological features that are essential for frigatebirds with regard to their aerial life in terms of staying aloft for months. Cumulus clouds are a characteristic pattern of the trade winds and play a major role for the flight behavior of frigatebirds.

The most important feature for the subject under consideration is that there are updrafts inside trade cumulus clouds and that these can be strong, featuring high speeds of the rising air (Roll, 1965). Updraft speeds inside trade cumulus clouds show a range of (Roll, 1965)

\[ w_{updraft} = 0.5\text{−}5 \text{ m/s} \]

An example is given in Fig. 1, based on in-flight measurement data (Malkus, 1954). The diagram shows how the updraft speeds are distributed across a cumulus cloud, involving a region with high updraft speed and a region where practically no updraft exists.

Further to trade cumulus cloud features that are important for frigatebirds, the cloud base is constantly at about 600 m to 700 m (Malkus, 1958). Trade cumulus clouds have a horizontal extension of about 100 m to 2 km and show a vertical thickness of about 300 m to 3 km (Malkus, 1958).

Another feature of trade cumulus clouds that is of importance is the availability of trade cumuli in regard to time as well as to location.

With respect to the time, trade cumulus clouds exist not only during daytime but also at night (Malkus, 1956). That differs from cumulus clouds over land which exist only during daytime and disappear at night. The fact that trade cumulus clouds show little di-
3.1.2. Characteristics of frigatebird flight paths inside and outside trade cumulus clouds

An illustrative presentation of the flight of a frigatebird inside a trade cumulus cloud is given in Fig. 3 which provides a perspective view of the 3-dimensional motion in the air space using measurement data and shows several ascents and glides. The highlighted ascent inside a cloud extends from the cloud base to an altitude of 2052 m at the top of the trajectory. The movement in the horizontal direction appears as a straight leg that is aligned with the wind. This is associated with the motion of the cloud which is drifting with the wind. The drift is due to the wind features of the trade wind zones where persistent strong winds exist. Further to Fig. 3, the highlighted ascent inside the cloud is followed by a glide outside the cloud. There is a difference in the direction of the glide compared to that of the ascent flight inside the cloud. This refers to the desired course in terms of the overall flight direction which is determined by the weighted combination of the directions of the flight portions inside and outside the cloud.

3.1.3. Flight properties of frigatebirds inside trade cumulus clouds

As reference that will be used for dealing with flight stability and control in the following chapter 3.2, it is shown that – and how – frigatebirds perform sustained flights inside clouds. It will be substantiated that these flights are ascents which consist of a soaring flight mode without flapping the wings.

For dealing with the non-flapping issue, an ascent inside a cloud is presented in Fig. 4. The time histories of wing flapping and altitude show that there is no flapping. An ascent without flapping
is only possible if there is an updraft that lifts the bird up. This can occur below or inside trade cumulus clouds, but not outside because no updrafts exist there. Further to ascent patterns, the altitude profile in Fig. 4 shows flights with low and high climb rates. The high climb rate is at 4.0 m/s whereas the low climb rates is at 0.5 m/s. The ascent with a high climb rate occurs in the altitude region above 600 m, and the ascent with a low climb rate is in the altitude region below. Since the base of trade cumulus clouds is constantly at about 600 m to 700 m (Malkus, 1958), it can be concluded that ascents involving a high climb rate are inside clouds. This is further supported by the fact that updraft speeds below trade cumulus clouds are so low (Siebesma et al., 2003; Malkus, 1954) that climb rates as high as 3.0 m/s to 4.0 m/s are impossible in that altitude region.

A sequence of ascending flights during a longer time period is presented in Fig. 5. This Fig. reveals how ascents below the cloud base and ascents inside clouds are distributed over the time for about 2 days. As regards flights inside clouds, Fig. 5 shows that frigatebirds perform those flights during daytime as well as at night. The highest ascent inside clouds reaching more than 4000 m shows a demanding environment at the top of the trajectory, involving freezing conditions as well as a substantial reduction of air density and oxygen to about 50% of the values at sea level (Weimerskirch et al., 2016).

In summarizing the climb performance as well as the frequency and regularity of frigatebird flights inside clouds, Fig. 6 shows the relationship between altitude and climb rate for a large number of ascents. Out of a total number of 1056 ascents each of which is indicated by a point, the number of ascents inside clouds amounts to 221, and the number of ascents below the cloud base amounts to 1035. As a result, a significant portion of the total number of the ascents is performed inside clouds. The altitude region where ascents of frigatebirds inside clouds take place extends up to the top of trade cumulus clouds. The highest ascent presented in Fig. 6 reaches an altitude that is even beyond 4 km. Characteristically for ascents inside clouds, the achievable climb rates are much larger than below clouds, yielding the following relations: climb rates below clouds were on average 0.41 ± 0.29 m/s below 600 m, and 1.86 ± 1.13 m/s above 600 m (F1,7 = 21.2, P = 0.006). This means that the climb rates inside the clouds are much higher, showing a factor of almost 5 when compared with the climb rates below the clouds. The data presented in Fig. 6 reveal that there are climb rates inside clouds nearing even 5 m/s. The presented results suggest that frigatebirds intentionally and regularly fly inside clouds. Because of the great number of ascents inside clouds, it can be concluded that frigatebirds are able to do this in a controlled and stabilized manner.

3.2. Stability and control of flight inside clouds

3.2.1. Control of circling ascents inside clouds

Ascents of frigatebirds associated with cumulus clouds show a flight mode consisting of circling soaring (Pennycuick, 1983; Weimerskirch et al., 2016; Rattenborg et al., 2016). By means of circling soaring, the birds are able to exploit the narrow thermals of cumulus clouds. This ability is supported by their exceptionally
Control of the undisturbed reference circling flight is accomplished by roll, yaw and pitch control moments which a bird can generate by appropriate changes of the wing shape (Pennycuick, 2008). Pitch control moments are produced by sweeping the wings forward and backward. Roll control moments are generated by pronation/supination at the wrist or humeral rotation. Yaw control moments are produced by shortening one wing so that the resulting drag vector of both wings is no longer acting at the body center of gravity, but at a point beside it to yield a moment about the vertical body axis.

Lateral control in circling flight is achieved with roll and yaw control moments which are required for the roll and yaw moment equilibrium conditions

\[ L = 0 \]
\[ N = 0 \] (4a)
to yield

\[ L_{\text{control}} + (\partial L/\partial r)r = 0 \]
\[ N_{\text{control}} + (\partial N/\partial r)r = 0 \] (4b)

where \( L \) is the roll moment, \( N \) is the yaw moment, \( r \) is the yaw rate and subscript “control” is used to indicate the control moments. For expanding the relations given by Eq. (4b), the roll and yaw moment coefficients are introduced, yielding

\[ C_l = \frac{L}{\rho V^2 S} \]
\[ C_n = \frac{N}{\rho V^2 S} \] (4c)

where \( S \) is the wing reference area, \( s \) is the half span of the wing and \( \rho \) is the air density. Using the moment coefficient notation, the solution for the roll and yaw control moments can be obtained in non-dimensional form as

\[ C_{l,\text{control}} = -\frac{sg \sin \phi}{V^2} C_{l,\text{ref}} \]
\[ C_{n,\text{control}} = -\frac{sg \sin \phi}{V^2} C_{n,\text{ref}} \] (4d)

where \( C_{l,\text{ref}} \) and \( C_{n,\text{ref}} \) are the derivatives of the moment coefficients in the roll and yaw axes due to the yaw rate, given by \( C_{l,\text{ref}} = \partial C_l/\partial (rs/V) \) and \( C_{n,\text{ref}} = \partial C_n/\partial (rs/V) \). There is also a pitch control moment input which the birds are supposed to be able to generate and which is not considered here. The roll and yaw control moments, \( C_{l,\text{control}} \) and \( C_{n,\text{control}} \), are set at constant values in terms of trim moments which describe the reference control status.

The question is how frigatebirds can maintain that reference circling flight in an environment that shows various effects influencing the motion and its control. Two conditions inside cumulus clouds are dealt with: Increased turbulence, and lack of visual cues.

a) An exemplary case of an increased turbulence level is graphically addressed in Fig. 8 which presents results on turbulence in- and outside a cumulus cloud from in-flight measurements (Malkus, 1954). The turbulence index shows how the turbulence level is increased inside the cloud compared to the region outside the cloud.

b) There is a lack of visual cues inside clouds. Thus, no visual cues are available for a frigatebird to acquire an orientation in space. Visual contact with the surface of the Earth is lost, and the horizon is not usable as a reference. Vision is the primary sense used to maintain equilibrium in birds (e.g., Warrick et al., 2002). In aerial vehicles, gyroscopic type instruments provide information on angular velocity and angular position so that spatial orientation in clouds is feasible. However, no biological sense organ providing a similar information is known in birds (Pennycuick, 2008).
It is assumed that sustained, controlled flight in cloud is not possible for birds (Pennycuick, 2008; Pennycuick, 1972; Dinevich and Leisem, 2010; Alersam, 1997).

A result of turbulence is that there are disturbance effects acting on the bird. According to the turbulence characteristics graphically presented in Fig. 8, the disturbance effects can be stronger inside clouds compared to outside clouds. A consequence of turbulence effects can be deviations from the reference flight path that the bird wants to follow. This is a matter of flight stability and control. While stability involves an inherent capability to act against deviations and to restore the flight condition existing before the disturbance, control means that the bird exerts purposeful control moments in pitch, roll or yaw aimed at counteracting the disturbances. The following sections address these issues and describe a mechanism that would allow a frigatebird to maintain circling flight in such a difficult environment.

3.2.2. Circling flight stability and control

Flight stability is determined by the modes of motion which include the short period, phugoid, roll subsidence, Dutch roll and spiral mode (Cook, 2007). It can be assumed that the short period, the phugoid and the roll subsidence are inherently stable modes of motion (Thomas and Taylor, 2001; Taylor and Thomas, 2002; Sachs, 2009; Sachs, 2007). This also holds for the Dutch roll though the birds are lacking a vertical tail which is an essential component for yaw stability (Sachs, 2007). Other than these modes, the spiral mode can show stability or instability. This is an issue for frigatebirds flying inside clouds.

Disturbances acting on a frigatebird produce deviations in the motion quantities from the circling reference flight condition dealt with above. Possible deviations from the reference circling trajectory manifest in the excitation of the spiral mode. An illustrative presentation of the spiral mode is given in Fig. 9 which shows how a lateral displacement (y) associated with a bank angle (Δφ) develops in the case of instability.

For dealing with the described scenario, it is assumed that the motion of a non-flapping bird can be dealt with in a similar way as the motion of a soaring aerial vehicle. Furthermore, for modelling the spiral mode, reference is made to a system associated with the wind which can be used as an inertial reference system assuming constant updraft and wind speeds. The equations of motion describing the spiral mode involve relations for sideward forces, roll moments and yaw moments (Cook, 2007), yielding

\[
mg\Delta\phi - mV \Delta r = 0
\]

\[
(\partial L/\partial \beta) \Delta \beta + (\partial L/\partial \phi) \Delta \phi + (\partial L/\partial r) \Delta r = 0
\]

\[
(\partial N/\partial \beta) \Delta \beta + (\partial N/\partial r) \Delta r = 0
\]

where \(m\) is the mass of the bird, \(\beta\) is the sideslip angle and \(\phi\) is the time derivative of the bank angle. The quantities \(\Delta r, \Delta \beta\) and \(\Delta \phi\) are the deviations from the corresponding quantities of the reference circling flight condition described by Eq. (4a). Applying the moment coefficient notation according to Eq. (4c), these relations can be expressed in non-dimensional form as

\[
\Delta \phi - (V/g) \Delta r = 0
\]

\[
C_{\phi \beta} \Delta \beta + C_{\phi \nu}(s/V) \Delta \phi + C_{\phi r}(s/V) \Delta r = 0
\]

\[
C_{\phi \nu} \Delta \phi + C_{\phi r}(s/V) \Delta r = 0
\]

where the stability derivatives \(C_{\phi \beta}, C_{\phi \nu}\) and \(C_{\phi r}\) are given by \(C_{\phi \beta} = \partial C_{\phi}/\partial \beta, C_{\phi \nu} = \partial C_{\phi}/\partial \nu\) and \(C_{\phi r} = \partial C_{\phi}/\partial r\), respectively.

The solution of the differential equation system Eq. (5b) shows that the spiral mode is of aperiodic nature. This yields for the bank angle

\[
\Delta \phi = A_{\phi} e^{t

where \(t\) is the time and \(A_{\phi}\) is a constant. The exponent \(s_1\) is the eigenvalue of the spiral mode and describes the time behaviour. It is decisive for the stability of the motion, yielding as criterion for stability

\[
s_1 < 0
\]

Examining Eq. (5b), \(s_1\) can be obtained to yield

\[
s_1 = \frac{g \left( C_{\phi \beta} C_{\phi \nu} - C_{\phi \beta} C_{\phi r} \right)}{C_{\phi r} C_{\phi \nu}}
\]

As a result, the stability of the spiral mode is determined by the relationships of the stability derivatives occurring in that expression. The stability derivatives show typical signs (Schlichting and Truckenbrodt, 2001). It is assumed that the following relationships hold for frigatebirds

\[
C_{\phi r} > 0, \ C_{\phi \beta} < 0, \ C_{\phi \nu} < 0, \ C_{\phi \beta} > 0, \ C_{\phi r} < 0
\]

Thus, for the stability criterion of the spiral mode

\[
C_{\phi r} - C_{\phi \beta} C_{\phi \nu}/C_{\phi \beta} < 0
\]

On the assumption that \(C_{\phi r}\) is smaller than the remaining term, the spiral mode can be regarded to be stable.

In addition to these basic stability characteristics, there is a unique combination of aerodynamics and size/mass properties in frigatebirds further improving the stability of the spiral mode. The aerodynamics property is relating to the form of the wings which feature a rather distinctive shape. As shown in Fig. 10, wings of frigatebirds are swept at the outer part which has a comparatively

![Fig. 8. Measurement results of turbulence in- and outside trade cumulus cloud (same case as in Fig. 1). The turbulence index in- and outside a trade cumulus cloud is presented, using measurement data given in Malkus (1954). The turbulence reaches high values inside the cloud, with considerable variations across the cloud. Compared with the conditions outside the cloud, the turbulence level inside the cloud is much higher.](image-url)

![Fig. 9. Spiral mode. The spiral mode is a mode of motion involving changes in the bank angle, \(\phi\), the yaw rate, \(r\), and the sideslip angle, \(\beta\), associated with a lateral displacement, \(y\), from the reference flight path. The scenario presented in Fig. 8 refers to the development of the bank angle deviation \(\Delta \phi\) and the lateral displacement \(y\) in terms of increasing values caused by a disturbance acting on the bird. The scenario with increasing values would correspond to an instability of the spiral mode, showing a continual growth of \(\Delta \phi\) and \(y\).](image-url)
high sweep angle of about 20\degree or even more. Sweep in wings yields an increase of the stabilizing influence of $C_B$ for which the following relation holding for constant-chord swept wings is indicative (Schlichting and Truckenbrodt, 2001)

$$C_B = -(\gamma/A + \eta_l \tan \lambda_{sweep}) C_L$$  \hspace{1cm} (11)

where $\lambda_{sweep}$ is the sweep angle, $C_L$ is the lift coefficient, $\eta_l$ is the lateral distance of the lift center of a wing from the symmetry plane, $A$ is the aspect ratio and $\gamma$ relates to the wing end form ($\gamma = 3/2$ for a straight wing end and $\gamma = 1.0$ for a rounded one). According to Eq. (8), an increase of $C_B$ in negative direction increases the magnitude of $s_0$. An increased magnitude of $s_0$ means that the restoring, stabilizing action in case of a disturbance is speeded up. This can be understood as a higher level of stability.

The other property of frigatebirds promoting spiral mode stability addressed above is wing loading, $mg/S$. According to Eq. (8), $s_0$ is proportional to the inverse of $V$, i.e. $s_0 \sim 1/V$. Using the lift expression in circling flight (with load factor $n$)

$$C_L = (\rho/2)V^2/n = mg/S$$  \hspace{1cm} (12)

for replacing $V$, the following relation equivalent to $s_0 \sim 1/V$ is obtained

$$s_0 \sim 1/\sqrt{mg/S}$$  \hspace{1cm} (13)

This relation shows that the magnitude of $s_0$ increases with a decrease in wing loading, $mg/S$. As a result, a low wing loading leads to a higher level of stability. Since frigatebirds have a very low wing loading (Pennycuick, 2008; Norberg, 2002), they profit from this in terms of a higher stability level.

To sum up, stability of the spiral mode provides an inherent restoring capability in terms of forces and moments that act against deviations. Thus, the reference flight condition can be restored, without needing a control action.

3.2.2.3. Effects of neutral azimuth stability on flight inside clouds

There is a further topic important for the flight of frigatebirds inside clouds. It is the ability to hold the course in a certain direction, given by the azimuth angle. This particularly applies to flights at zero visibility and without a visual reference, as it is the case inside clouds.

The azimuth angle is the motion quantity that describes the course of a bird. Thus, it is an important quantity for directional orientation and navigation. With regard to straight and level flight, the following relation which can be obtained from motion quantities described in Eq. (6a, b) holds for the azimuth angle

$$\chi = \int r \, dt + \beta$$  \hspace{1cm} (14)

According to this relation, there are no restoring force or moment effects if a deviation in the azimuth angle occurs. Correspondingly, flying objects, be it birds or aircraft, have basically no inherent stability with respect to the azimuth angle. Rather, they feature only neutral stability (Cook, 2007). Neutral azimuth stability means that a perturbation in the azimuth angle results in a deviation from the desired course. This deviation is maintained in the steady-state because there is no inherent force or moment that act against it in order to restore the azimuth state before the perturbation.

Neutral azimuth stability is an issue for straight flight. This notably holds for migrating birds trying to keep course in a given direction. With regard to straight flight, a consequence of a deviation in the azimuth angle is that there is a translational displacement from the desired flight path that continually increases, as graphically addressed in Fig. 11. The translational displacement can be described by

$$y = \int V \sin \Delta \chi \, dt$$  \hspace{1cm} (15a)

where $\Delta \chi$ is the azimuth deviation. In the case of a constant azimuth deviation, the increase of the translational displacement from the desired flight reads

$$y = V \sin \Delta \chi \cdot t$$  \hspace{1cm} (15b)

Thus, an active control input counteracting the deviation is necessary to reduce the translational displacement to zero. For being able to exert a corrective control input, a reference for the desired flight path is required.

In visual flight conditions, there is a reference for the desired flight path so that a corrective control action appropriate for restoring the desired azimuth and course can be performed. When flying inside clouds, however, visual references are not existent. Therefore, birds would have to rely on other cues and a sense organ that could provide the respective information of azimuth (for example, a magnetic sense). Without a reference that provides the required precision, a corrective control action does not lead to the intended goal. As a result, a translational displacement from the desired flight path would continually increase. All in all, sustained and controlled flight inside clouds is assumed not to be possible for birds (Pennycuick, 2008).

Concerning circling flight of frigatebirds inside trade cumulus clouds, the relationship between an azimuth angle deviation and a change in the flight path is basically different from that existing in straight flight. This is graphically addressed in Fig. 12 where a circling flight scenario is presented. In Fig. 12a, a perspective view on the flight path before and after a translational displacement is depicted. In Fig. 12b which is used for modelling the translational
displacement, a topview of the circling flight is presented where the condition before an azimuth deviation $\Delta \chi$ is indicated applying dotted lines (flight path and speed), while solid lines are used for the flight thereafter. The speed direction change given by the azimuth deviation $\Delta \chi$ leads to an offset of the circling flight path in the lateral and longitudinal directions. This can be described by the following relations

\[
\begin{align*}
\Delta x_{\text{center}} &= R_c (1 + \sin \Delta \chi) \\
\Delta y_{\text{center}} &= R_c \cos \Delta \chi
\end{align*}
\]  

where $\Delta x_{\text{center}}$ and $\Delta y_{\text{center}}$ are the offsets of the circling center and $R_c$ is the circling radius given by Eq. (3a). The translational displacement in terms of $\Delta x_{\text{center}}$ and $\Delta y_{\text{center}}$ does not increase, but is limited and remains constant. This constancy in the translational displacement is due to the circling motion which prevents that $\Delta x_{\text{center}}$ and $\Delta y_{\text{center}}$ increase. Thus, there is a fundamental difference from straight flight. As a result, the bird can continue circling after a disturbance at a position that is adjacent to the former circling.

With regard to the translational displacement that may occur during circling flights of frigatebirds inside clouds, the size of the circling radius in relation to the horizontal extension of cumulus clouds is important. According to Eq. (16), the translational displacements $\Delta x_{\text{center}}$ and $\Delta y_{\text{center}}$ are the smaller the smaller the circling radius. Frigatebirds have an advantage because they feature a low circling radius which is small when compared with other birds. This is due to their low wing loading, $\text{mg/s}$. Observations reveal that the circling radius of frigatebirds is of the order of 10 m (Pennycuick, 1983; Pennycuick, 2008). Compared to this, updrafts in trade cumulus clouds show horizontal extensions that are much larger (for example, the horizontal extension of the updraft presented in Fig. 1 is about 1000 m). Therefore, a limited translational displacement in the circling motion as shown in Fig. 10 can well stay within the updraft of a trade cumulus cloud. As a result, a circling ascent inside a cumulus cloud can be continued after an azimuth deviation without the necessity of a corrective control action. This implies that there is no energy gain penalty.

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