

École polytechnique de Louvain

The role of muscular fatigue in position swaps during collective bird migration

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Abstract

This thesis is part of the RevealFlight Project. This project aims to understand the efficiency optimization mechanisms deployed by biological flyers through the study of the aerodynamics, mechanics and control laws of birds. In particular, this work focuses on the role of muscular fatigue in position swaps during collective bird migration. In the first place, the aerodynamics of a bird is examined in order to understand how migratory birds can take advantage of the upwash created by the bird in front of him. However, muscles cannot work all the time with the same efficiency. The three-compartment muscle fatigue model sheds light on the principle of endurance time, time before a muscle feels fatigued. A simple muscle model is then presented in order to simulate the distribution of the kinematics and dynamics of a bird into its passive and active elements. Finally, these models are put together so that the dynamics and kinematics of a bird can be simulated in order to obtain the endurance time of a bird. The impact of the velocity on the endurance time of a bird is analyzed as well as the difference between birds flying alone and birds flying in a flock and taking advantage of the upwash region.

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Chapter 1

Introduction

This work is part of the RevealFlight Project. This project *aims at shedding light on the efficiency optimization mechanisms deployed by biological flyers. We will focus on birds, and in particular on migratory birds, which are known to exhibit such efficiency-seeking mechanisms at several levels, while maintaining relatively stable flight conditions, leading to impressive results* [1]. This thesis analyzes the behavior and interaction between migratory birds when they fly in a flock. The impact of the velocity on the power as well as the relative position between 2 birds will be discussed. The simulation code for the aerodynamics is provided by Gennaro Vitucci, postdoctoral researcher at UCLouvain.

In addition, light is shed on the muscle fatigue phenomenon. Every individual has, at least once in his life, experienced fatigue. When someone goes for a run or plays a sport, he feels that its force production decreases with time and with the intensity of the physical exercise. The moment when he can no longer generate a desired force is called the endurance time. In other words, it is the period during which muscles do not feel fatigued. After this period, the force production starts to drop. This model is able to simulate constant and oscillating force demand. Different parameters will be studied and linked to the endurance time in order to determine the optimum parameters.

A simple muscle model is then proposed in order to link the muscle fatigue with the aerodynamics of a bird. All these models together are able to simulate the dynamics and kinematics of a bird. The influence of a bird's speed can be analyzed with these models. The difference in power and endurance time between solo flights and tandem flights will be discussed during this thesis.

Chapter 2

Aerodynamics of a bird

This chapter will focus on how a bird manages to fly. The aerodynamics of the bird will be explained in order to understand the forces acting on a moving bird. It is followed by an explanation of the interaction between birds flying in a flock. The physics behind this composition will be explained and discussed.

Afterwards, the musculoskeletal composition of a bird will be explained. This gives a better understanding of which muscles are involved during the different strokes of a wing-beat.

This chapter ends with a discussion over the bird's power and wing-beat frequency. The impact of the velocity on the power will be shown. The saved power by the follower will be discussed in function of its position and velocity. All the results in this chapter come from a code developed within the UCLouvain project RevealFlight by Doctor G. Vitucci.

2.1 Methodology

2.1.1 Aerodynamic power

During this entire work, I assume that the bird flies at a constant speed and horizontally (it stays at the same height). When the bird is moving in the air, several forces are acting on his body [2]:

- his weight caused by the action of the gravity on its mass, $m \cdot g$
- the lift, L , caused by the relative motion between the bird and the air. L is perpendicular to the incident airflow.
- the drag, D , force opposite to the direction of motion and it is the resistance of the air acting on the bird's body. D is in line with the airflow.
- the thrust, T , force that a bird has to generate in order to fly at a constant speed. Birds generate this force by flapping their wings.

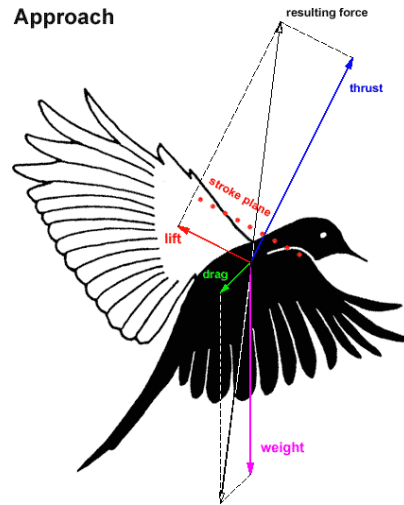


Figure 2.1: Forces acting on a bird [3]

Figure 2.1 illustrates the forces acting on a bird. As the bird is not accelerating, we notice that the sum of all the forces is equal to 0 [N]. Lift balances the weight while thrust balances drag.

To fly, birds create a downward momentum to the air and obtain lift by reaction. This can be explained with Newton's third law, which says that the action and reaction forces are equal and opposite to each other. The lift depends on several parameters: the body shape, the inclination, the air viscosity, etc. In order to simplify this dependencies, scientists introduced the lift coefficient, C_L which characterizes these parameters. For thin airfoils and at small angle of attack, C_L is directly proportional to the angle of attack, α , expressed in radians [4]. The angle of attack is the angle formed by the reference line on the wing and the oncoming flow.

$$C_L = 2\pi \cdot \alpha \quad (2.1)$$

Wings have several degrees of freedom but in this thesis, I use only 2 of them. It can flap around a hinge representing the body. This angle is called θ and can be seen as the angle formed by the wing and a vertical line passing through the center of the bird. It can also rotate around the humerus bone in order to adjust the angle of attack, α . In the code made by G. Vitucci, postdoctoral researcher at UCLouvain [5], θ is expressed as:

$$\theta(t) = K \cdot \left(\frac{1}{2} + \sin\left(\frac{2\pi}{T}t\right) + \Phi_t \right) \quad (2.2)$$

This degree of freedom depends on the period of oscillation, T , the phase shift Φ_t and an other parameter, K . Moreover, the angle of attack is related to θ . It can be expressed as:

$$\alpha = \arctan\left(\frac{b}{2v} \frac{d\theta}{dt}\right) + A \quad (2.3)$$

In this equation b is the wingspan which represents the maximal distance between the wing-tips, v the velocity of the bird and A an other parameter. This equation can be inserted in equation 2.1 in order to obtain the value of the lift coefficient, C_L . A and K are control parameters that ensure that the bird is always in equilibrium. Indeed, the sum of all the forces acting on the bird must be equal to zero.

The general equation of lift, L , depends on the air density, ρ [kg/m^3], the airspeed, v [m/s], the surface area of the wing, S_{wing} [m^2] and the lift coefficient, C_L [-].

$$L = \frac{1}{2} \cdot \rho \cdot v^2 \cdot S_{wing} C_L \quad (2.4)$$

When a bird moves its wings in the air, it generates lift but also drag. The drag can be seen as the friction between the bird and the airflow. Drag can be separated into 2 portions: the induced drag and the parasite drag. The difference between these 2 terms is the surface area they enter in contact with. The induced drag is the drag generated by the lift while the parasite drag is the drag generated by the frontal area of the bird against the air. Both drags depend on the air density, ρ [kg/m^3] and the airspeed, v [m/s]. The induced drag also depends on the surface area of the wing, S_{wing} [m^2] and the induced drag coefficient, $C_{D,ind}$ [-] while the parasite drag depends on the frontal surface area, S_{front} [m^2] and the parasite drag coefficient, $C_{D,para}$ [-].

$$\begin{aligned} D_{ind} &= \frac{1}{2} \cdot \rho \cdot v^2 \cdot S_{wing} C_{D,ind} \\ D_{par} &= \frac{1}{2} \cdot \rho \cdot v^2 \cdot S_{front} C_{D,par} \end{aligned} \quad (2.5)$$

It appears that the induced drag coefficient, $C_{D,ind}$ is linked to the lift coefficient, C_L , the wingspan, b , the wing area, S_{wing} , and an induced power correction factor, k [2]. The induced drag coefficient can be expressed as:

$$C_{D,ind} = \frac{k C_L^2}{\pi \frac{b^2}{S_{wing}}} \quad (2.6)$$

The area of the wing, S_{wing} can be expressed as the wingspan, b , times the mean chord, c_m [2]. The chord of a wing is the width of a wing. So the area of the wing can be seen as a rectangle with the wingspan as length and mean chord as width.

The frontal area of the bird depends on the mass of the bird [2]:

$$S_{front} = 0.00813 \cdot m^{2/3} \quad (2.7)$$

Optimally designed wings bring the air from upstream to downstream with the smallest amount of momentum loss, loss of drag, as possible and the highest lift as possible [6].

The aerodynamic power for a bird can be estimated by the sum of the induced power, P_{ind} , the parasite power, P_{par} , the profile power, P_{pro} , climb power, P_{climb} and acceleration power, P_{acc} :

$$P_{aero} = P_{ind} + P_{par} + P_{pro} + P_{climb} + P_{acc} \quad (2.8)$$

All the equations presented here are taken from paper [7] and paper [2].

The parasite power is defined as the rate at which work must be done to overcome the parasite drag.

$$P_{par} = D_{par} \cdot v = \frac{1}{2} \cdot \rho \cdot S_{front} \cdot C_{D,par} \cdot v^3 \quad (2.9)$$

The induced power is the rate at which the bird has to provide work, in order to support his weight. It depends on a constant, the induced power correction factor k , the downwash induced velocity, w [m/s] and the mass of the bird.

$$P_{ind} = k \cdot w \cdot mg \quad (2.10)$$

In the case of a horizontal flight, the downwash induced velocity can be expressed in terms of the wingspan, b [m], the bird's speed, v [m/s] and the air density, ρ [kg/m³]:

$$P_{ind,hor} = k \cdot \frac{2 \cdot (mg)^2}{v\pi b^2 \rho} \quad (2.11)$$

The profile power is the work needed to overcome the induced drag.

$$P_{pro} = D_{ind} \cdot v = \frac{1}{2} \cdot \rho \cdot S_{wing} \cdot C_{D,ind} \cdot v^3 \quad (2.12)$$

The climb power is defined as the change in potential energy and the acceleration power is defined as the change in kinetic energy. As we assumed that the altitude and speed are constant, these 2 contributions of the aerodynamic power are equal to 0 [W].

In this case, the aerodynamic power from equation 2.8 becomes:

$$\begin{aligned} P_{aero} &= P_{ind} + P_{para} + P_{pro} \\ &= k \cdot \frac{2 \cdot (mg)^2}{v\pi b^2 \rho} + \frac{1}{2} \rho v^3 S_{front} C_{D,para} + \frac{1}{2} \rho S_{wing} C_{D,ind} v^3 \end{aligned} \quad (2.13)$$

We notice that the aerodynamic power strongly depends on the velocity, v . When v increases the contribution of the induced power decreases while the contributions of the

parasite and profile power become important. The cost of producing lift decreases while the cost to overcome the parasite and profile drag increases with a forward velocity. For small velocities, the induced power, P_{ind} is the major component. The parasite power, P_{para} , and profile power, P_{pro} become more important when birds fly faster.

The aerodynamic power presents a velocity for which the required power is a minimum. This velocity is called the minimum power speed and is denoted as v_{mp} . If a bird flies at this speed, it needs to generate a minimal power. v_{mp} can be found by differentiating equation 2.13 and setting the first derivative equal to zero [8].

$$\frac{dP_{aero}}{dv} = -\frac{2k(mg)^2}{\pi b^2 \rho} \frac{1}{v^2} + \frac{3}{2} v^2 \rho (S_{front} C_{D,para} + S_{wing} C_{D,ind}) = 0 \quad (2.14)$$

The minimum power speed, v_{mp} can be expressed as:

$$v_{mp} = \left(\frac{4}{3\pi}\right)^{1/4} \cdot \left(\frac{k}{S_{front} C_{D,para} + S_{wing} C_{D,ind}}\right)^{1/4} \cdot \left(\frac{mg}{b\rho}\right)^{1/2} \quad (2.15)$$

This speed can be seen as the "rock-bottom power"; that is the lowest power with which the bird can conceivably remain airborne [8].

There is also a speed for which the bird can achieve a maximum range. This speed is denoted as v_{mr} . For a maximum range, the distance travelled per unit work done must be maximized. This ratio will be referred to as the specific range, $E = \frac{v}{P}$ where P is the power required to fly at that velocity v [8]. In order to find the speed for which the range is maximized, it is the same to find the speed for which $\frac{1}{E}$ is a minimum.

$$\frac{1}{E} = \frac{P}{v} = k \cdot \frac{2(mg)^2}{v^2 b^2 \rho} + \frac{1}{2} \rho v^2 S_{front} C_{D,para} + \frac{1}{2} \rho S_{wing} C_{D,ind} v^2 \quad (2.16)$$

From this equation, v_{mr} can be found by differentiating $1/E$ and setting the first derivative equal to 0.

$$\frac{d(\frac{1}{E})}{dv} = \frac{2k(mg)^2}{\pi b^2 \rho} \frac{(-2)}{v^3} + \rho (S_{front} C_{D,para} + S_{wing} C_{D,ind}) v \quad (2.17)$$

v_{mr} can be expressed as:

$$v_{mr} = \left(\frac{4}{\pi}\right)^{1/4} \cdot \left(\frac{k}{S_{front} C_{D,para} + S_{wing} C_{D,ind}}\right)^{1/4} \cdot \left(\frac{mg}{b\rho}\right)^{1/2} \quad (2.18)$$

When we compare v_{mr} to v_{mp} , we notice that they are proportional. In fact, the velocity for which the range is maximal, is 1.316 times greater than the minimum power speed.

$$v_{mr} = 1.316 \cdot v_{mp} \quad (2.19)$$

These 2 specific velocities will be of interest when the aerodynamic will be coupled with the fatigue model.

2.1.2 Interaction between multiple birds

When looking at migration birds, we notice that they sometimes fly in a flock. The most common flock patterns are the V-formation or cluster [9]. We will focus on the v-shaped formation because the bird of interest in this work is the Bald Ibis (*Geronticus eremita*) and these birds fly in a v-shaped formation when they migrate [10]. Birds fly in this particular formation in order to protect themselves against predators, to share orientation and information and also to reduce their energy consumption. In a flock, there is always a leader, which is at the beginning of the flock and leads the other birds. The other birds, called followers, are placed behind him so that they can take advantage of the moving air induced by the leader. A common "hypothesis" is that this happens because of upwash exploitation. When birds fly, they produce lift by creating a pressure difference between the top and bottom of their wings. However, this pressure difference cannot be maintained beyond the wingtips, as there is no longer a surface to create the pressure gradient. As the air is moving from a high pressure region to a low pressure region, there is a stream of air trailing from the wingtip which is called the upwash [9]. This also creates a downwash region which is located behind the main body of the bird. Birds place their wingtip in the upwash region in order to take advantage of air flow moving upwards and so to save energy. This particular positioning also helps birds to avoid the downwash region which leads to an increasing energy consumption.

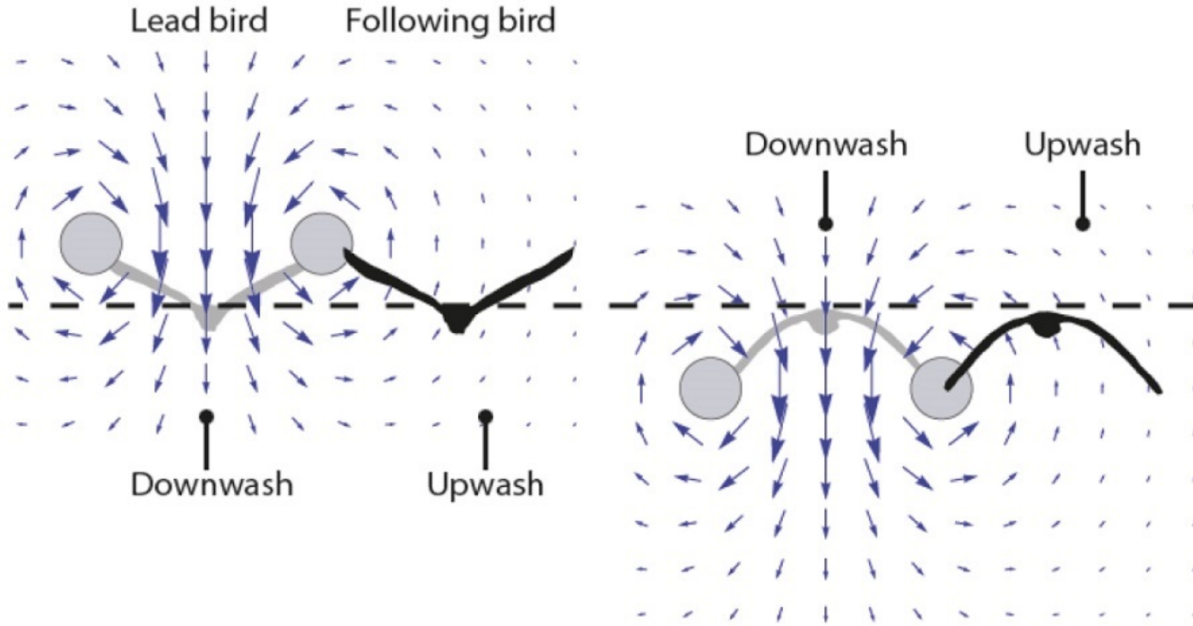


Figure 2.2: Representation of the position of the following bird to take the most advantage of the upwash [10]

Figure 2.2 shows how the follower takes advantage of the upwash region created by the leader. The arrows represent the direction and magnitude of the airflow. We see that in the region behind the bird's body, the airflow is directed in the downward direction while in the

region behind the wingtip, the airflow is directed in the upward direction. The key to take the most advantage of the upwash is the position of the follower compared to the leader. A good way to evaluate the position is the wingtip spacing, s . Wingtip spacing is defined as the distance between the 2 wingtips of the 2 birds. s can be positive (the wings do not overlap) or negative (the wings overlap each other). The optimal value for the wingtip spacing can be expressed as:

$$s_{opt} = -0.11 \cdot b \quad (2.20)$$

So the overlap zone of the follower and leader is 0.11 times their wingspan [11]. According to theoretical calculations based on fixed-wing theory, followers can save up to 50% of their power when flying at the optimal wingtip spacing in the upwash region compared to when they are flying alone. However, in reality, follower birds can save up to 15% of their power generation by flying in a V-shaped formation [9]. The wingtip spacing and position of the follower depends on the formation of the flock and the bird's specie.

Furthermore, the process of capturing the upward airflow is not passive. The birds coordinate their wing flaps with a phase shift mechanism such that their wingtips always follow the path of the front bird's wingtips. This active behavior allows the following birds to maximize the capture of the beneficial upwash and so reducing their required power [12].

2.1.3 Flight muscles of birds

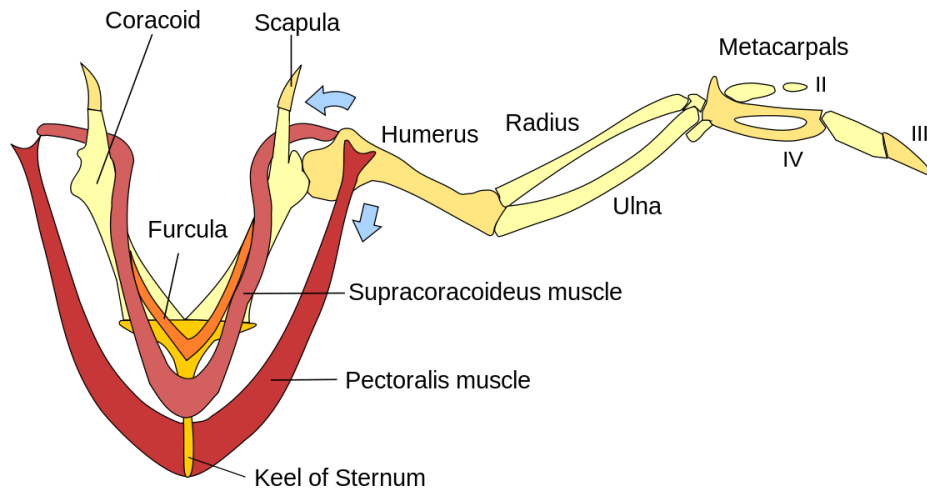


Figure 2.3: Skeletal and musculature structure of a bird's wing [13]

In order to fly, a bird counts many muscles. However, it mainly generates its power with only 2 muscles: the pectoralis and supracoracoideus muscle. These 2 muscles can be seen as the engine of the bird. Figure 2.3 shows where the muscles are located in a bird. The pectoralis muscle is the largest muscle of the wing and is attached to the humerus bone [14]. When the pectoralis muscle contracts, it pulls the humerus bone down. This downward

movement is called the down stroke. During the down stroke, the feathers overlap so the air can't pass through which results in lift [6]. On the other hand, the supracoracoideus, which is also connected to the humerus, acts like a pulley. It lifts the wing upwards every time the muscle contracts. This movement is called the up stroke. During the up stroke, the feathers turn so the total surface of the wing decreases. This lets air pass through in order to decrease the needed energy. The upstroke can be seen as the recovery stroke. The power is mostly generated during the down stroke.

When looking at the bird's muscles, we notice that they are located below the wing, as shown on figure 2.3. This specific feature helps to stabilize birds as the center of mass is compact and located below the wing.

2.2 Results

All the results presented in this section come from a code made by G. Vitucci, postdoctoral researcher at UCLouvain. This code takes into account all the aerodynamic forces acting on a bird. The input are the bird's motion: speed, flapping frequency, etc. It can also simulate several birds flying in a flock. So we can see how much energy is saved by a follower by flying in the upwash region. We can also play with the number of birds composing the flock and the distance between them. I used this code to simulate the power generated by a bird, to simulate the internal stress applied by the wing on the bird's center of mass and also to analyze the impact of the different parameters on the power consumption.

In this code, some assumptions are made in order to make the code less complex while keeping a certain level of precision. The assumptions are:

- The bird's wings are assumed to be linear and stiff (there is no degree of freedom between the humerus bone and the radius and ulna bones).
- The bird is also assumed to be symmetrical: the 2 wings undergo the exact same motion.
- If there are more than 1 bird, the birds are identical : same mass and same dimension.
- The speed is constant.
- The altitude is also kept constant.

Each migration bird species have their own wingbeat frequency. However, they are all in the same order of magnitude. It varies between 2.75 Hz to 10.8 Hz [15]. Figure 2.4 shows the evolution of the angle formed by the wing and a vertical line passing through the center of the mass of the bird, denoted θ in the previous section, during 3 flaps. In this figure, the frequency is set at 3 [Hz]. We notice that the shape of the angle's curve is, according to the equation 2.2, a sinusoidal. The down stroke is when the angle decreases and the up stroke is when the angle increases. The second graph of figure 2.4 shows the power generation of

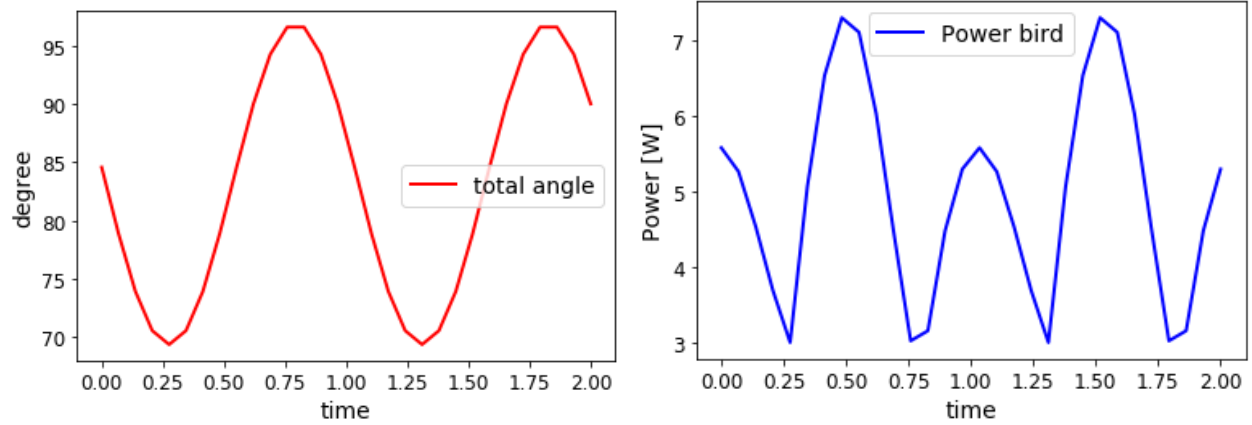


Figure 2.4: Evolution of the angle of a bird's wing and the power generated by the bird with a velocity of 10 [m/s] and a wingbeat frequency of 3[Hz]

the bird also during 3 wingbeats. We can notice that during the down stroke, birds need to generate more power while during the up stroke, the power is reduced.

Impact of the velocity on power and range

Figure 2.5a shows the evolution of the aerodynamic power as a function of the velocity. We notice that the power as function of the velocity is, as expected, in a U-shape. The black cross shows the velocity at which the power is at its minimum. In this case, v_{mp} is 9 [m/s]. The red cross indicates the speed at which the bird will achieve a maximal range as explained in section 2.2.1. v_{mr} is equal to 13 [m/s] as it is illustrated in figure 2.5b. We notice that the relationship between v_{mr} and v_{mp} explained in equation 2.19 is more or less preserved. In our case, v_{mr} is 1.44 times greater than v_{mp} . We also notice that the power difference at these 2 speeds is relatively low. The minimum power, P_{mp} , is equal to 4.95 [W] while the power to achieve the maximum range, P_{mr} is equal to 5.90 [W]. P_{mr} is 1.19 times greater than P_{mp} . When we look at the range-velocity relationship in figure 2.5b, we notice that for small velocities, the ratio P/v increases strongly. We see that the range achieved by a bird flying at its minimum power velocity, is slightly bigger than the range at the minimum range velocity even though $v_{mp} < v_{mr}$.

When we look at the effective power generated by the muscles of the birds, we notice that the muscle power-velocity relationship is similar to the aerodynamic power-velocity relationship. It also presents a U-shape curve as shown on figure 2.6. It shows the mass-specific power of the pectoralis muscle since it is the primary muscle supplying the mechanical power output required for flight. This figure shows also that the power generated by the muscles strongly depends on the bird specie and flight style.

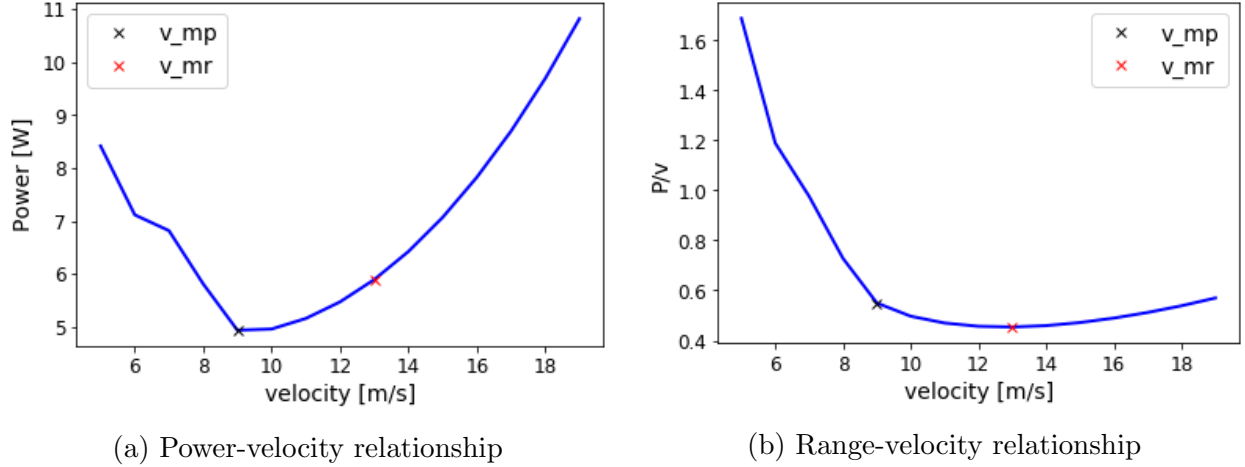


Figure 2.5: Frequency=3 [Hz], mass=1 [kg]

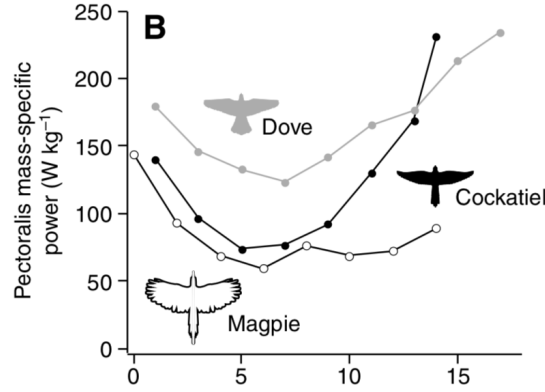


Figure 2.6: Pectoralis mass-specific power and velocity for different birds [16]

Saved Power

Now we will have a look at the energy saved by the follower when it flies in the upwash region behind the leader. The difference between the power generated by a single bird, P_{solo} , and the power generated by the follower, P_f divided by the single bird's power is of interest in this section.

$$\text{Saved power}_f = \frac{P_{solo} - P_f}{P_{solo}} [\%] \quad (2.21)$$

Figure 2.7 shows the relationship between the saved power and velocity. We notice that the saved power decreases when the speed increases. This is due to the fact that when the follower flies in the upwash region created by the leader, the upward airflow helps to reduce the induced power of the follower. As we can see in equation 2.13, the induced power is inversely proportional to the velocity. Moreover, as we assumed that all the birds are identical, the parasite and profile power do not change compared to the leader. This is the reason why the saved power decreases when the speed increases. A bird following a leader flying at a constant speed of 6 [m/s] needs 43% less of the total power. For a speed of 20 [m/s], the follower saves less than 8% compared to a bird flying alone.

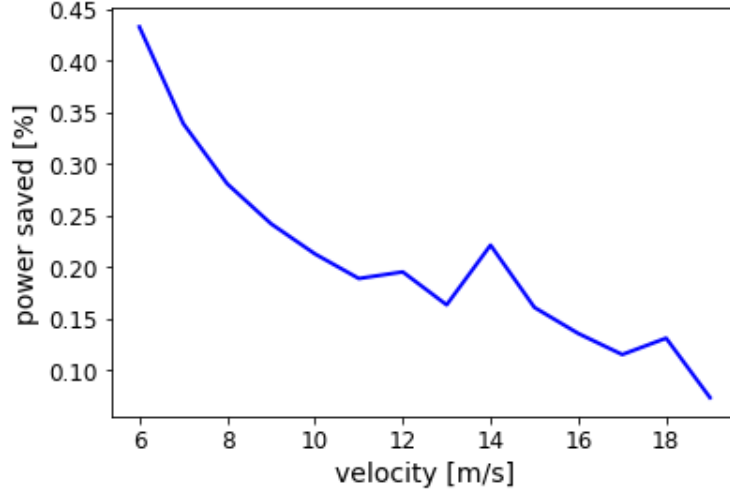


Figure 2.7: Saved power versus velocity

Wingtip spacing

In this section, I will study the behavior of the Bald Ibis (*Geronticus eremita*). Bald Ibis fly in a v-shaped formation. The follower is located from 0.49m to 1.49m behind the leader according to an experiment lead by Steve J. Portugal [10]. He studied a free-flying flock of 14 bald ibises and measured the position, speed and heading of all birds in the formation as well as their wingbeat frequency. The experiment lasted 43min and data were taken with back-mounted synchronized GPS (5Hz) and inertial measurement units (300Hz). It appears that they mostly stay 1.2m behind the leader [10]. He also analyzed the wingtip spacing between 2 following birds. It appears that bald ibis have a preference of wingtip spacing of -0.115m which represents 0.0958 times their wingspan. This value is in the range of the predicted optimal wingtip spacing. The flight parameters of the bald ibis are presented in table 2.1. Figure 2.8 shows the energy saved-wingtips spacing relationship. We notice that the saved energy is maximal for a wingtip spacing of -0.13 times the wingspan. This value is different from the expected optimal value but is still in the same order of magnitude. However, we notice that the reduction of power between the follower and leader is below the expectation. The follower can at most save 7.61% of the power generated by the leader. This value is lower than the 10 to 14 % according to Steve J. Portugal [9].

Figure 2.9 shows the relation between the depth (distance in the x-direction between the follower and leader). The optimal depth according to experiments on bald ibis is 1.2m. Most of the time, they are located at a distance from 0.5m to 1.5m behind the leader. According to this simulation, the optimal distance between 2 birds is 2 [m] which lays not in the range of 0.5 [m] to 1.5 [m]. At this depth, the follower saves 16.75% of his power. This value is in the same order of magnitude (slightly higher) as the value proposed by Steve J. Portugal according to whom a bird can save up to 15% by flying in the upwash region created by the bird in front of him. Also we notice that a depth of 0.5 m to 0.6m has a negative impact on the power of the follower. If the follower flies in this region, it has to generate more power which is not the desired goal of flying in a v-shaped formation.

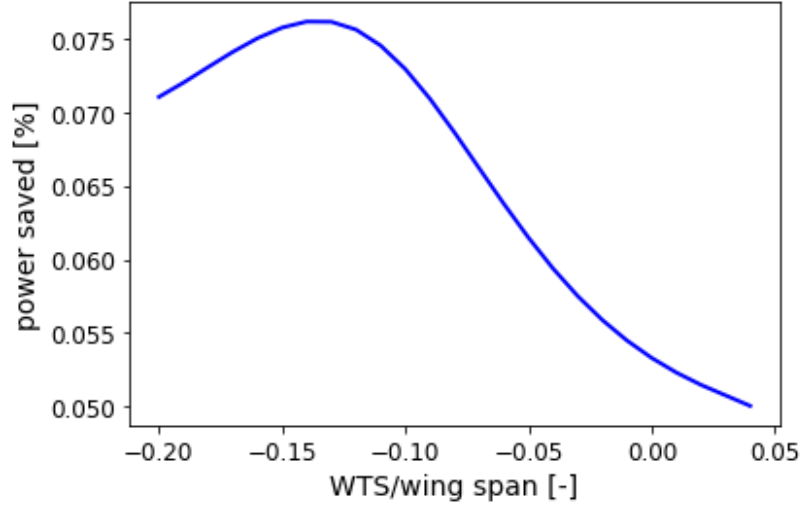


Figure 2.8: Power saved-wingtips spacing relationship for a depth of 1.2m, velocity of 14 m/s and wingbeat frequency of 4 Hz

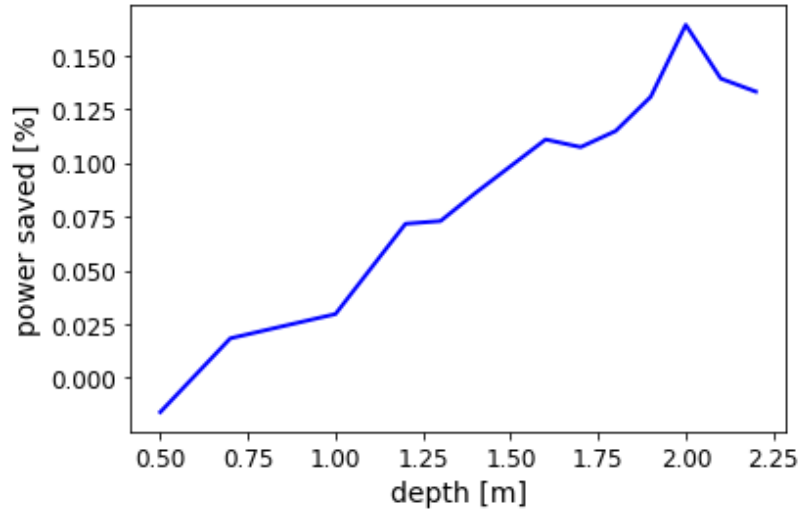


Figure 2.9: Saved power - depth relationship, $s = -0.13 \cdot b$

	Bald Ibis
Wingspan [m]	1.2
Depth [m]	0.49-1.49
Optimal s [m]	0.115 (from 0 to 0.13)
Flight speed [m/s]	14
Wingbeat frequency [Hz]	3-4

Table 2.1: Flight parameters for a Bald Ibis [\[11\]](#)

2.3 Conclusion

We have seen that the velocity plays an import role in the required aerodynamic power of a bird. The power-velocity curve presents a minimum for which the required power is minimal. However, by flying at this velocity, a bird will not be able to attain a maximal range. The maximal range velocity is slightly bigger than the minimum power velocity. We have also seen that the position of the follower in relation to the leader has a real impact on the power saved by the follower. In order to save the most power, a bald ibis flying at 13 [m/s] has to be 2 [m] behind the leader and their wingtips have to overlap over a distance of 0.13 times their wingspan. If the follower achieves to fly at this position, a bald ibis is able to save up to 20% of the power required by the leader.

All these results are taken from a code provided by G. Vitucci, postdoctoral researcher at UCLouvain, as part of the RevealFlight Project.

Chapter 3

Fatigue model

This chapter focuses on the fatigue model. The fatigue phenomenon is part of our daily life but it is a very complex phenomenon. When you do some physical exercises, you notice that after a certain amount of time, you start to feel tired: when you run, you cannot keep the same speed for an infinite period. After an intense exercise, you feel tired/exhausted. Sometimes, the day after, you still have sore muscles. This means that muscles do not recover instantaneously. The amount of time needed to recover, as well as the time to become fatigued, depends on the intensity of the activity.

This chapter starts with a description of previous fatigue models. I will explain the choice of the three-compartment muscle fatigue model followed by a physical description of this model. Then the impact of the intensity of the task will be discussed. The fatigue and recovery rates will also be analyzed. This chapter ends with a discussion and analysis of the frequency-endurance time relationship.

3.1 Introduction

Muscle fatigue is a very complex phenomenon. It is a result of many physiological and neurological processes occurring simultaneously. It is impossible to identify one universal mechanism responsible for the drop of the force.

Researchers first tried to demonstrate muscle fatigue by using empirical approaches. This kind of approach relies on experimental results. However, it depends on the accuracy of the experiment setup and it is very difficult to perform different tasks with a reasonable accuracy. Also it cannot be generally applied to more complex tasks [17].

Then, scientists tried theoretical approaches. These approaches use already known muscle models. One or several decay terms are added to the model in order to simulate the fatigue phenomenon. This kind of approach is complex but useful at a single muscle level. However, several physiological and biomechanical parameters need to be determined. The number of parameters varies between 15 and more than 30 depending on the model. It is the reason why this kind of approach has been dropped.

In 2002, the first motor-unit based fatigue model was proposed by professor Jing Z. Liu [18]. It relies on biophysical principles and is based on 3 muscle-activation states: resting state, fatigue state and activated state. This model has only 3 parameters and 1 input variable. This simple model is suitable for data fitting and more general applications. However, it does not work under dynamic conditions.

The model I study in this chapter is based on the motor-unit based model. It is called the three-compartment muscle fatigue model. It also has 3 parameters: a fatigue coefficient, F , a recovery coefficient, R , and a feedback controller, $C(t)$. This model happens to be consistent with muscle physiology and joint biomechanical properties, is capable of predicting fatigue for simple and complex tasks at varying intensities and is computationally efficient [17].

3.2 Methodology

Each muscle is composed of several muscle units, MU. One muscle unit can be divided into 3 different activation states: resting state (M_r), activated state (M_a) and fatigued state (M_f). A muscle is never in a fixed state, it has a dynamic behavior. There is an interaction between the different states as it is shown on figure 3.1.

In order to produce a force, a sufficient part of the muscle unit must be fully tensioned. When a muscle state is fully tensioned, it means that it is activated. However, a muscle cannot be in full tension for an infinite time. After a certain amount of time (proportional to the inverse of the fatigue coefficient, F), the available force decreases. The activated muscle states become fatigued. In order to simplify the model, when a muscle becomes fatigued, its tension is defined as equal to zero. So the force generated by a group of muscle units is proportional to the size of the activated muscle states.

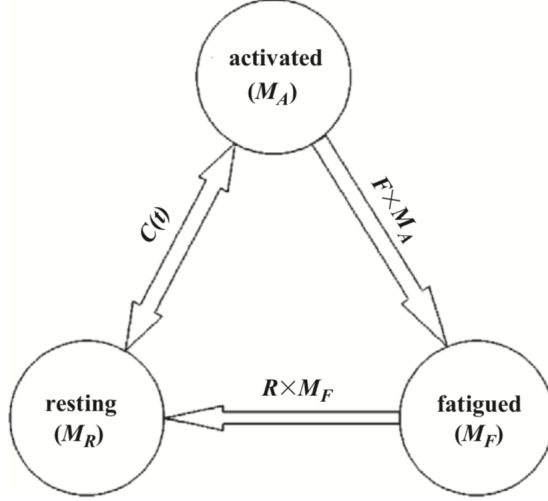


Figure 3.1: Dynamic behavior of a homogeneous muscle unit pool [17]

On the other hand, when a portion of the muscle unit is fatigued, it can recover and be in a resting state. The rate at which a fatigued muscle state can recover is called the recovery coefficient, R . The tension of the resting muscle states is assumed to be 0. The resting states are muscle states that are not activated and not fatigued. They can be activated by the activation-desactivation drive, $C(t)$. Once they are activated, they are fully-tensioned and generate a force. A resting state will be activated if the intensity of the target load cannot be achieved by the current activated muscle state. Moreover, an activated muscle state can return to its resting state if the available activated state manages to produce the desired target load. This is possible with the use of the activation-desactivation drive, $C(t)$.

In this model, when we speak of force, we use the definition of target load:

$$TL = \frac{F_{current}}{F_{max}} \quad (3.1)$$

The target load is the ratio of the total force that the muscle unit is able to produce and the total maximum force that the muscle unit can produce [19]. TL will always be smaller than or equal to 1. A value of 1 means that all the muscle states need to be activated in order to generate the desired force.

Equation 3.2, equation 3.3 and equation 3.4 describe the interaction between the different states where F is the fatigue coefficient, R the recovery coefficient and $C(t)$ is the time-varying muscle activation-desactivation drive.

$$\frac{dM_a}{dt} = C(t) - F \cdot M_a \quad (3.2)$$

$$\frac{dM_f}{dt} = F \cdot M_a - R \cdot M_f \quad (3.3)$$

$$\frac{dM_r}{dt} = -C(t) + R \cdot M_f \quad (3.4)$$

The initial condition must satisfy that the sum of M_a , M_f and M_r is equal to 1. For the purpose of this thesis, we assume that at the beginning all the muscle unit is resting and no muscle is activated nor fatigued. The initial conditions for this system are:

$$\begin{cases} M_a(0) = 0 \\ M_f(0) = 0 \\ M_r(0) = 1 \end{cases}$$

As said before, $C(t)$ varies with time but it also depends on whether M_a achieves the target load and the availability of M_R :

$$\begin{cases} \text{If } M_a < TL \text{ and } M_r > TL, & C(t) = (TL - M_a) \\ \text{If } M_a < TL \text{ and } M_r < TL, & C(t) = M_r \\ \text{If } M_a \geq TL, & C(t) = (TL - M_a) \end{cases}$$

3.3 Results

As we can see on figure [3.2](#), at the beginning, M_a follows the target load perfectly. However, after a certain amount of time, M_a decreases. This means that the muscle unit is not able to produce the desired intensity given by the target load. This moment is called the endurance time (ET) and is a very important concept. The endurance time can be defined as:

$$\text{if } M_a(t) + M_r(t) < TL(t), \quad ET=t$$

As we can expect from the appellation, the unit of the endurance time is seconds. The endurance time depends on the target load and how fast the muscle becomes fatigued and how fast it can recover. This will be discussed in the next sections.

Also, the percentage of fatigued muscle increases gradually with the time as the muscles of the unit get more and more tired and can no longer produce the desired intensity. This is due to the fact that the recovery rate is smaller than the fatigue rate. So per unit of time, more states will become fatigued than will recover.

Figure [3.2c](#) shows the evolution of the different muscles states for a pulsing target load. We notice that when TL is equal to zero, the activated muscle states drop to zero. However, M_f and M_r do not drop to zero. When TL=0, the proportion of fatigue muscle states does not drop instantaneously to 0. This is due to the fact that the fatigued states do not recover instantaneously but decrease slightly. The activated states drop to zero so no more additional fatigued states appear during this period. So the number of fatigue states that recover is equal to the recovery coefficient, R, times the amount of time. We also notice that the proportion of the recovery states increases slightly.

On figure [3.2a](#), figure [3.2b](#) and figure [3.2c](#), in those 3 different cases, the endurance time is different. It is respectively of 25.5 seconds, 25.2 seconds and 50.3 seconds. For these cases,

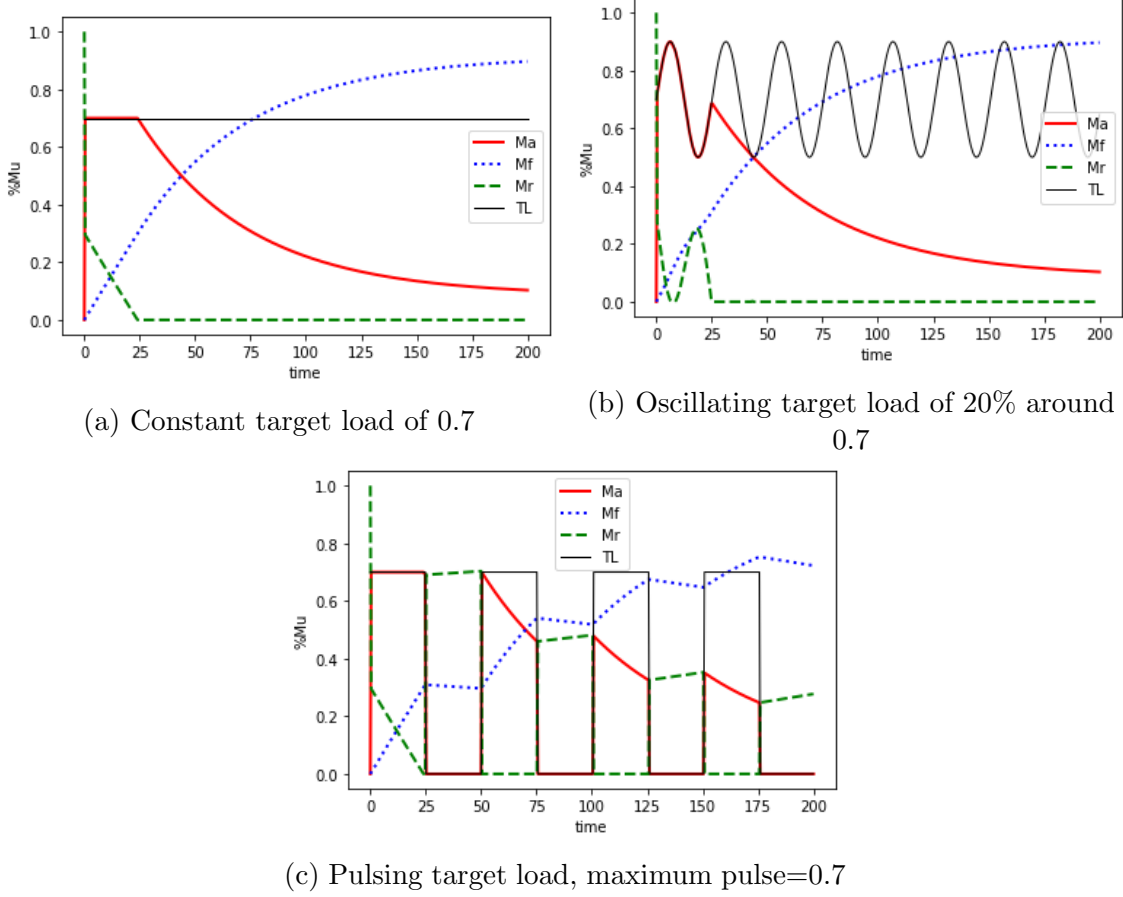


Figure 3.2: Distribution of muscle unit into active (M_a , red), fatigued (M_f , blue) and resting (M_r , green) states

the fatigue and recovery coefficient are set to $0.0182[\frac{1}{s}]$ and $0.00168[\frac{1}{s}]$ respectively. They are the optimal coefficient for the shoulder of a human [20].

When looking at figure 3.2a and figure 3.2b, we notice that when M_a can no longer follow the target load, it decreases but it never drops to 0. In fact, M_a decreases until it reaches an asymptotic value [20]. This asymptotic value can be expressed as:

$$M_{a,asymptotic} = \frac{1}{\frac{F}{R} + 1} \quad (3.5)$$

To obtain this value, $\frac{dM_a}{dt}$ is assumed to be equal to 0. So equation 3.2 can be rewrite as:

$$\frac{dM_a}{dt} = 0 \Leftrightarrow F \cdot M_a = C(t) \quad (3.6)$$

The next assumptions in order to obtain the asymptotic value are that $\frac{dM_r}{dt} = 0$ and $M_r = 0$.

$$\begin{aligned} \frac{dM_r}{dt} = 0 &\Leftrightarrow C(t) = R \cdot M_f \\ M_r = 0 &\Leftrightarrow M_f = 1 - M_a \end{aligned} \quad (3.7)$$

By combining equation 3.7 with equation 3.6, we obtain the equation for the asymptotic value of M_a . The asymptotic value depends only on the fatigue and recovery coefficient. It does not depend on the target load at all. An increase of R has a positive impact while an increase of F will have a negative impact on the asymptotic value. This asymptotic value is the same for constant, oscillating and pulsing target loads as long as F and R are the same. If the target load is below this asymptotic value, the muscle unit will never experience the fatigue phenomenon.

3.4 Parameters analysis

3.4.1 Target load

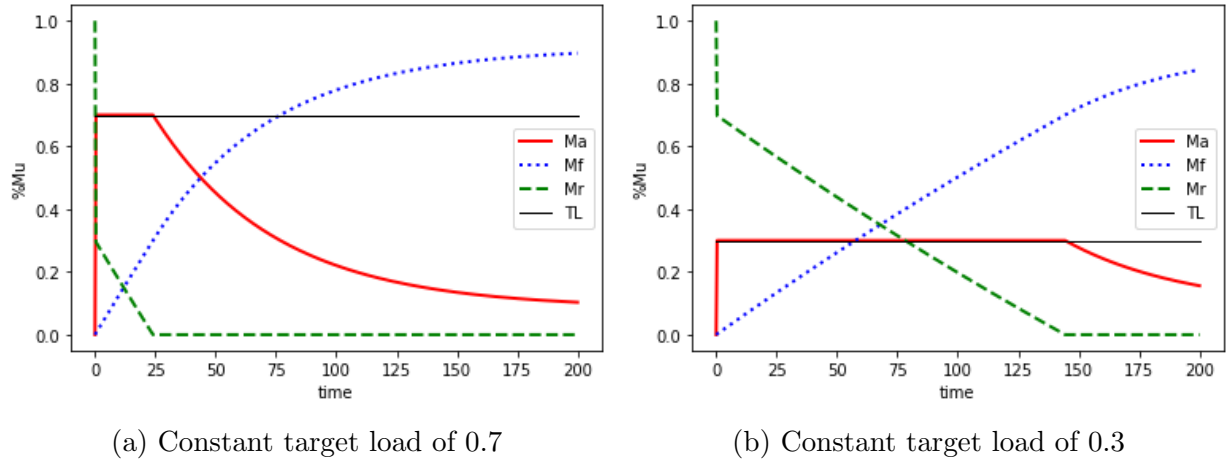


Figure 3.3: Evolution of M_a , M_f and M_r for a different constant target load

As said before, the target load influences the endurance time. As the target load increases, the endurance time becomes shorter. A constant TL of 0.3 has an endurance time of 148.3 seconds and a constant TL of 0.7 in the same conditions has a endurance time of 25.5 seconds. Indeed, with a higher target load, a more important part of the muscle unit must be activated. If the intensity is higher, then the activated muscle part becomes fatigued faster and so it cannot generate power anymore. Figure 3.4 is the generalization of the evolution of the endurance time versus the intensity of a constant target load. We notice that the ET is not directly proportional to the intensity. When the intensity decreases, the ET increases rapidly. We notice that figure 3.4 gives the same results as figure 3.3.

Figure 3.4 also illustrates the asymptotic value of M_a from equation 3.5. It clearly shows that for target load smaller than this asymptotic value, the system has no endurance time. Hence, the motor unit will never become fatigued. For shoulder muscles, the asymptotic value is equal to 0.0845 (see table 3.1).

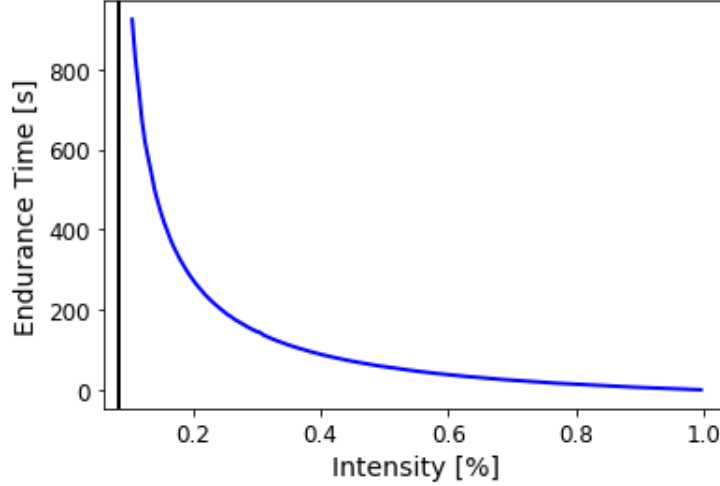


Figure 3.4: Endurance time versus Intensity [20]. The black line represents the asymptotic value of M_a , ref to equation 3.5.

3.4.2 Fatigue and recovery coefficient

As a remainder, F is the fatigue coefficient. It is the rate at which the activated muscle states become fatigued. R is the recovery coefficient and is the rate at which the fatigued muscle states recover.

Joint region	F [1/s]	R [1/s]	F/R
Ankle	0.00589	0.00058	10.2
Knee	0.01500	0.00149	10.1
Trunk	0.00755	0.00075	10.1
Shoulder	0.0182	0.00168	10.8
Hand/Grip	0.0098	0.00064	15.3
Elbow	0.00912	0.00094	9.7

Table 3.1: Value for the fatigue and recovery coefficients for different joint region [20]

F and R have unique value depending on the joint region. Some muscle may have a bigger tendency to become fatigued faster while some may be more resistant to fatigue. In the human body, shoulder muscles and knee muscles become fatigued faster than ankle muscle, trunk muscle and elbow muscle. When looking at the recovery rate, R in table 3.1, we notice that when F is higher, R is also high. This means that F and R are linked. In fact, in the human body, the ratio is more or less constant. It varies from 9.7 for elbow muscles to 15.3 for the hand/grip muscles. In average, the fatigue coefficient has a value of 0.0097[1/s] in the human body and the recovery coefficient has a mean value of 0.00091 [Hz]. The mean value of $\frac{F}{R}$ for the human body is 10.7 [20].

As said before, F is the fatigue coefficient and is the rate at which the activated states become fatigued. In another way, the inverse of F ($\frac{1}{F}$) is the time needed for the activated

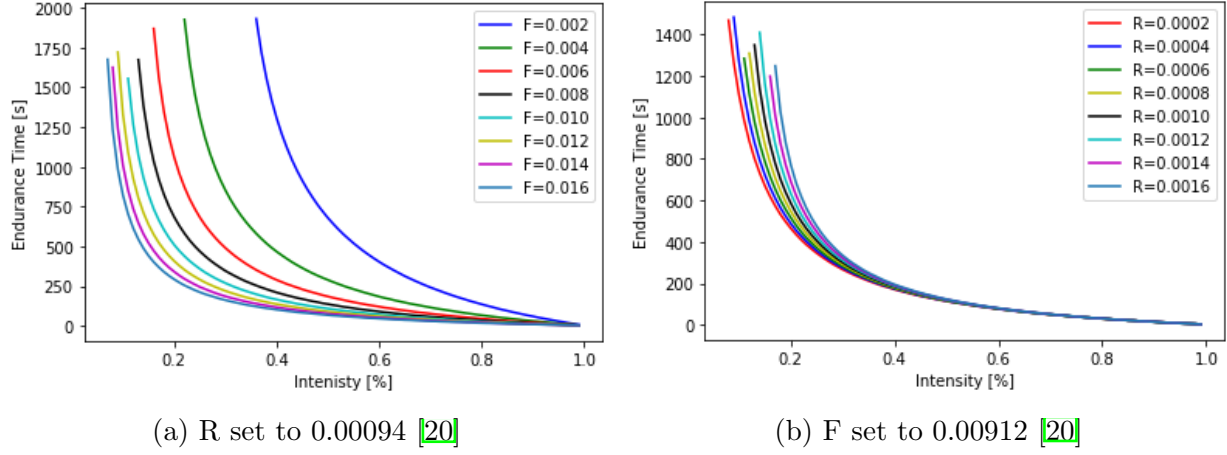


Figure 3.5: Impact of the fatigue and recovery coefficient on the endurance time [20]

state to become fatigued. As F increases, the fatigue rate increases and so the time to change of state becomes shorter. For a large value of F , the activated muscle states will stay less in that state than for a smaller F . So the endurance time will decrease because the muscle unit will not be able to produce the desired target load. Figure 3.5a illustrates this perfectly. For an intensity of 0.6, the endurance time is 423 seconds for $F=0.002$ and 192 seconds (less than the half) for $F=0.004$. Also for an endurance time of 400 seconds, there is a difference of 44% in intensity between the lowest F and highest F .

On the other hand, R is the recovery coefficient. It is the rate at which the fatigued states can recover and become resting states, M_r . In another way, the inverse of R ($\frac{1}{R}$) is the time needed for a fatigued state to recover and become at rest. As R increases, the recovery coefficient increases. So the time to change of state becomes shorter and more fatigued states can recover. It has a positive effect on the endurance time because it increases the proportion of available muscle states that can be activated. Figure 3.5b shows the endurance time versus intensity for different values of R . As expected, for an intensity of 0.3, the endurance time when $R=0.0002$ (280 seconds) is smaller than the endurance time when $R=0.0016$ (356 seconds). However, for an intensity of 0.8 or more, the recovery coefficient has no more effect on the endurance time. For those intensities, even if some fatigued states recover, this is not enough to compensate the lack of active muscle states in order to generate the desired force.

3.4.3 Ratio $\frac{F}{R}$

In table 3.1, we saw that in the human body the ratio $\frac{F}{R}$ is not constant, it varies from joint region to another. However, this ratio is in the same order of magnitude. In this section, we will investigate the influence of the value of $\frac{F}{R}$ on the endurance time.

If R is greater than F , so that $\frac{F}{R} < 1$, it means that there are more fatigued states that recover than activated muscle states that become fatigued per unit of time. This would mean that the individual never experiences the fatigue phenomenon when doing an activity, even

the most intense. However, this does not exist in nature.

The value of $\frac{F}{R}$ varies from 9.7 to 15.3 in a human body depending on the joint region. Figure 3.6 illustrates the impact of $\frac{F}{R}$ on the endurance time for different constant target loads. The value of $\frac{F}{R}$ runs from 8 to 16.5 in order to take into account all the value of the ratio in a human body and to see what happens for lower and higher value. When the ratio's value increases, it means that the proportion of fatigue muscle states in the muscle unit increases. On the other hand, when the ratio's value decreases, the proportion of fatigue muscle states in the muscle unit decreases compared to higher ratio's values.

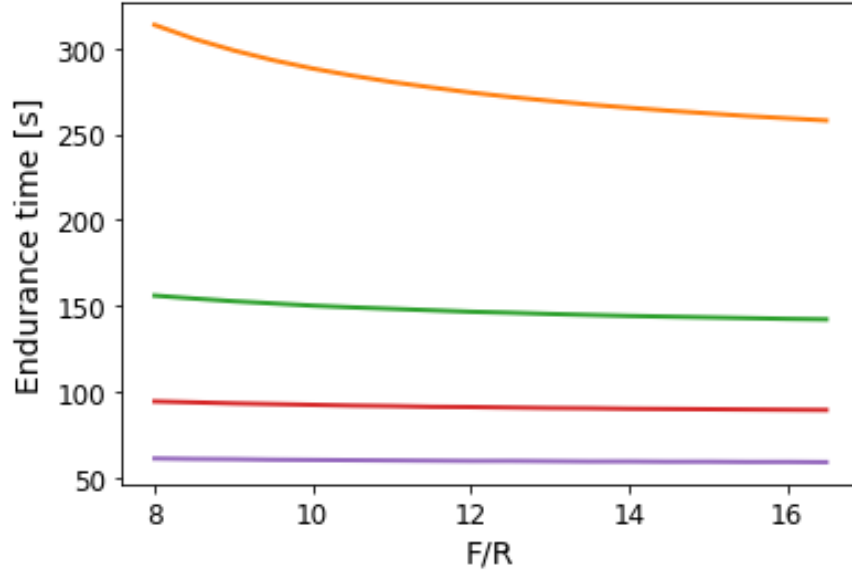


Figure 3.6: Impact of the ratio F/R on the endurance time for $TL=0.2$ (orange line), $TL=0.3$ (green line), $TL=0.4$ (red line) and $TL=0.5$ (purple line)

As we can see, for high target loads, $TL \geq 0.3$, the endurance time remains constant and so does not depend on the ratio's value. For these intensities, the variation of the proportion of the fatigued muscle states has no impact on the endurance time. For a given target load, the proportional increasing amount of recovery states (when $\frac{F}{R}$ decreases) is not sufficient in order to maintain the desired intensity in the muscle unit.

We also see on figure 3.6 that ET increases for low value of $\frac{F}{R}$ and low TL because the required amount of activated muscle states to maintain the level of intensity is low. So the small increase of the recovery states per unit of time is able to maintain a necessary amount of activated states to maintain the intensity longer compared to higher value of $\frac{F}{R}$. This is only possible for low target loads.

3.4.4 Frequency

As I am looking at the impact of fatigue on bird, it is interesting to analyze the reaction of the endurance time not only for constant target loads but also for dynamic target loads. Indeed, when a bird is flapping, its internal torque and power do not stay constant but vary and oscillate according to the wingbeat frequency and velocity. In this section, the impact of the frequency of an oscillating target load on the endurance time will be discussed.

The wingbeat frequency of a bird depends on the specie as well as on the type of flight. However, the wingbeat frequency of migration bird lays between 2.75 [Hz] and 10.8 [Hz] [15]. So I simulate the endurance time for this range of frequency. Figure 3.7 illustrates the variation of the endurance time due to an oscillating target load. The difference in mean target load is also shown on figure 3.7. The value of F and R are 0.01820 [Hz] and 0.00168 [Hz] respectively, values for the human shoulder.

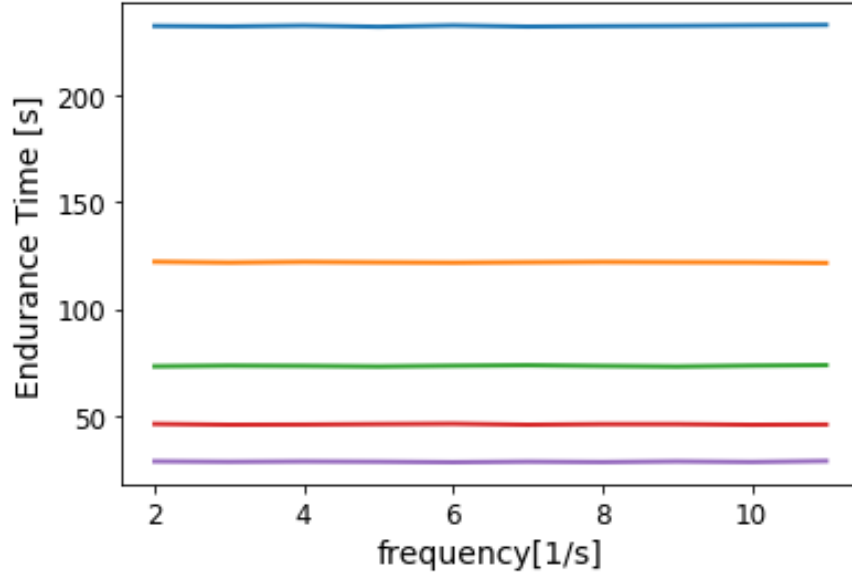


Figure 3.7: ET-frequency relationship for an oscillating target load: $TL = 0.1 \cdot \sin(2\pi f \cdot t) + TL_{mean}$. The different value of TL_{mean} are 0.2 (blue line), 0.3 (orange line), 0.4 (green line), 0.5 (red line) and 0.6 (red line)

The result is quite surprising because we see that the frequency does not play a role on the endurance time. Indeed, it is the mean value of TL that has an impact on the endurance time. This can be explained by the difference in timescales between the recovery and fatigue coefficient and the frequency. The recovery rate is around 0.001 times the frequency and the fatigue rate is around 0.01 times the frequency.

$$\begin{aligned} F &= \mathcal{O}(freq \cdot 10^{-2}) \\ R &= \mathcal{O}(freq \cdot 10^{-3}) \end{aligned}$$

One period of the target load ranges from 0.5 to 0.1 [s] while the period of the F and R are 54.95 and 595.24 [s]. So during 1 period of TL, the fatigue and recovery coefficients can

not have a significant impact on the proportion of activated, fatigued and recovered muscle states. Only the average value of the target load is significant as it determines the level of intensity and by extension the proportion of M_a .

In the case of oscillating target load, the frequency has no impact on the endurance time if the oscillation happens at a much higher frequency than the fatigue/recovery rates, as it is the case for humans. We can assume the target load to be constant and equal to its average value in order to determine the endurance time.

3.5 Conclusion

The fatigue phenomenon is very complex. However the three-compartment muscle fatigue model manages to simulate this phenomenon in a simple yet accurate way since the model is based on biophysical principles. The most important concept of this model is the endurance time, moment when the motor unit can no longer maintain the desired level of intensity. We saw that the intensity of the target load has an impact on the endurance time. A muscle unit can have an infinite endurance time if the intensity of the target load is lower or equal to an asymptotic value that depends on F and R . In order to obtain a long ET, TL has to be as close as possible to this asymptotic value. The fatigue and recovery coefficients and their ratio also has an impact on the endurance time. Finally, we saw that the endurance time does not depend on the frequency of an oscillating target load. Only the intensity matters. So for that kind of target load, we can assume the target load to be constant and equal to the average value of the target load. This is due to the difference in timescales between the frequency and F and R . This phenomenon will be useful when the fatigue model will be coupled with the bird's aerodynamics and muscle model in Chapter 5.

Chapter 4

Muscle model

The last model that is needed to fully understand the behavior of a bird, is a muscle model. A muscle model describes the kinematic and dynamic of muscles.

This chapter starts by explaining the mechanism behind skeletal muscle contraction. A simple muscle model is used to describe this behavior. It takes its total length and total force as input. However, since we are focusing on birds, we need to adapt this model in order to switch from a force and length model to a torque and angle model. This is why an equivalent system is needed. A clear explanation is given on how to switch from the so-called linear muscle model to the angular muscle model.

This chapter ends with a discussion on the results of both models.

4.1 Muscle contraction

Before jumping into the muscle model, it is important to understand the mechanism behind the muscle contraction. First of all, there exist 3 different kinds of muscle: skeletal muscles, cardiac muscles and smooth muscles. Skeletal muscles are attached to bones and allow voluntary movement of the body, cardiac muscles are only present in the heart and smooth muscles are found in the walls of hollow organs like the stomach, intestines, urine bladder and uterus and allow involuntary movement of parts of these organs [21]. Since we are focusing on wing movements, we will focus on the skeletal muscles.

The muscle contraction of skeletal muscles is based on the cross-bridge theory and was first introduced by A.F. Huxley in 1957 [22].

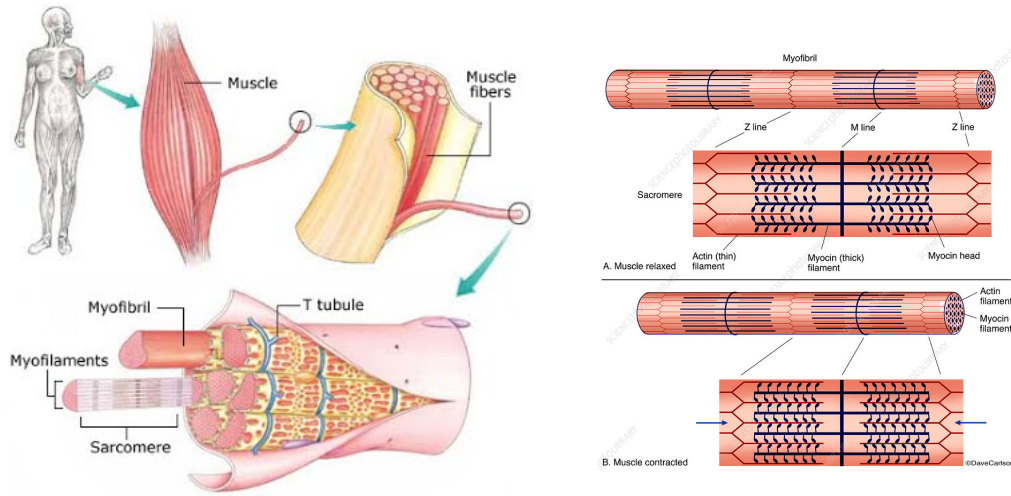


Figure 4.1: Muscle composition and cross-bridge theory ([23], [24])

A skeletal muscle is composed of blood vessels, connective tissues and fascicles. Fascicles are made of several muscle fibers. It is in the muscle fibers that the cross-bridge theory takes place. A muscle fiber is mostly composed of myofibrils which are responsible for muscle cell contraction and has a periodic structure. One period of the structure is called a sarcomere. In a sarcomere, there are thick filaments, called myosin filaments, and thin filaments, called actin filaments as figure 4.1 illustrates it. Cross-bridges are fixed in a regular pattern on the myosin filament. By cyclically bonding the cross-bridge heads to binding sites on actin filaments, the muscle fiber shortens and causes muscle contraction. During an attachment/detachment cycle, the cross-bridge head is thought to undergo a rotation and so pull the actin filament relative to the myosin. This pulling force leads to muscle shortening. By summing all the force acting on all the cross-bridges head, we can compute the total muscle contraction force. Figure 4.1 shows the difference between a relaxed and contracted muscle. We see that for a contracted muscle, all the cross-bridges heads are connected to the binding sites while for the relaxed muscle, some of the cross-bridges heads are not connected. The contraction level is related to the number of cross-bridge connections.

4.2 Methodology

A muscle can be schematized with a contractile element, CE, and 2 elastic elements [25]. One elastic element is placed parallel to the contractile element. It represents the elastic tissue parallel to the contractile part of the muscle fibers. This element is called, parallel elastic element, PE. The second elastic element is placed in serie to CE and PE. It represents all elastic tissue in serie to the muscle fibers. This element is called the serie elastic element, SE. Figure 4.2 represents this muscle model. The contractile element is the active element of the model.

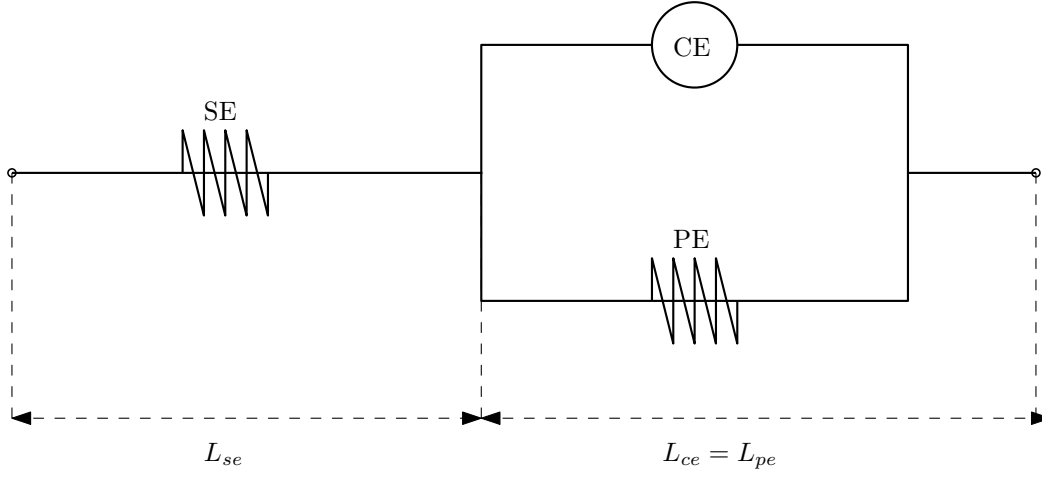


Figure 4.2: Linear muscle model

From the figure 4.2, we can derive equations 4.1 and 4.2. They are based on the mechanical properties of the elements.

$$dL = dL_{se} + dL_{ce} \quad (dL_{ce} = dL_{pe}) \quad (4.1)$$

$$F = F_{se} = F_{ce} + F_{pe} \quad (4.2)$$

Now let's focus on the force produced by the system when we impose a known length, L . For the purpose of this study, the contractile element will be considered as a black box which provides the force of the contractile element. From equation 4.1 and from the fact that the serie element is an elastic with stiffness, k_{se} , the variation of the lengths of the different element of the system can be obtained.

$$\begin{aligned} dL_{se} &= L_{se0} + \frac{F}{k_{se}} \\ dL_{ce} &= dL - dL_{se} \end{aligned} \quad (4.3)$$

By knowing the variation of the length of the active element (which is the same as the length of the parallel elastic element), the force required by the active element can be expressed as:

$$F_{ce} = F - k_{pe} \cdot dL_{ce} \quad (4.4)$$

However, the contractile element does not produce a force all the time. It generates a force only when it is contracted, only when $\Delta L_{ce} > 0$. In other words, L_{ce} has to be smaller than the resting length, $L_{ce,0}$ to generate a force. If it is not the case, then $F_{ce} = 0$ [N]. To resume:

$$\begin{cases} \text{If } \Delta L_{ce} > 0 : & F_{ce} = F - k_{pe} \cdot \Delta L_{ce} \\ \text{If } \Delta L_{ce} < 0 : & F_{ce} = 0 \end{cases} \quad (4.5)$$

Since we are focusing on birds, we are interested in the torque produced by the muscle. We need to adapt figure 4.2 in order to achieve this task. Figure 4.3 is the angular representation of the muscle model. It is still composed of a contractile element, CE, in parallel with an elastic element, PE. These 2 elements are in serie with an other elastic element, SE. However, the stiffness of the elastic elements are now expressed in [N·m/rad]. We adapt the linear model by replacing force with torque and length with angle.

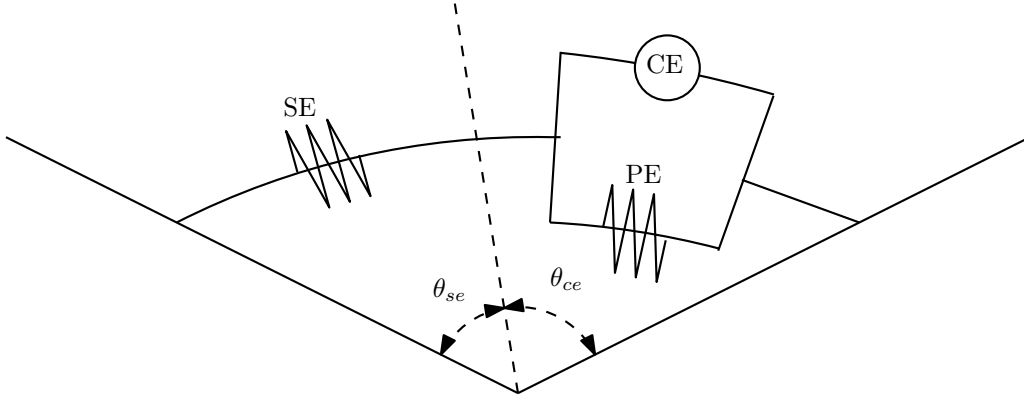


Figure 4.3: Angular form of the muscle model

So equation 4.1 and equation 4.2 become:

$$d\theta = d\theta_{se} + d\theta_{ce} \quad (d\theta_{ce} = d\theta_{pe}) \quad (4.6)$$

$$T = T_{se} = T_{ce} + T_{pe} \quad (4.7)$$

With the same logic as for the derivation of the variation of the total force for the linear Hill's muscle model, the final expression of the contractile torque, T_{ce} can be expressed as:

$$T_{ce} = T - k_{pe} \cdot \Delta\theta_{ce} \quad \text{with } \Delta\theta_{ce} = \theta_{ce0} - d\theta_{ce} \quad (4.8)$$

Although the active element does not produce a torque all the time. It generates a torque only in contraction, only when $\Delta\theta_{ce} > 0$. Otherwise, $T_{ce} = 0$ [N.m]. To resume:

$$\begin{cases} \text{If } \Delta\theta_{ce} > 0 : & T_{ce} = T - k_{pe} \cdot \Delta\theta_{ce} \\ \text{If } \Delta\theta_{ce} < 0 : & T_{ce} = 0 \end{cases} \quad (4.9)$$

4.2.1 Choice of the parameters

Now that we have the equations to solve the muscle model, we still need to determine the parameters. To solve the system, 3 parameters are present:

- stiffness of the parallel elastic element, $k_{ang,pe}$
- stiffness of the serie elastic element, $k_{ang,se}$
- angle at rest, θ_0

Determination of the angular stiffness

We need to determine the angular stiffness, k_{ang} of the elastic and parallel elements, $k_{ang,se}$ and $k_{ang,pe}$. They need to response to the dynamics of the problem. To do so, an equivalent model is needed because data on k_{ang} are not available. The goal is to retrieve them from data on linear muscle models. The equivalent model simulates the force of the shoulder generated by the pectoralis and supracoracoideus muscles on the center of the bird. Figure 4.4a shows the experiment setup. The distance is defined as the distance between the center of the bird and the head of the humerus bone. Figure 2.3 shows the representation of a bird's wing. So this distance can be seen as the resting length of the pectoralis muscle. As explained below, if one expresses the angular stiffness from equivalence, they are non-linear and time-dependent.

For this experiment, we assume that one of the muscle model is rigid and does not move. A force, dF , is applied to the muscle model. This force will create a shortening or elongation of the total length, dL , depending on the direction of the force. An angle, $d\alpha$ is created as the result of this deformation. Figure 4.4b illustrates reaction of the system to a contraction force.

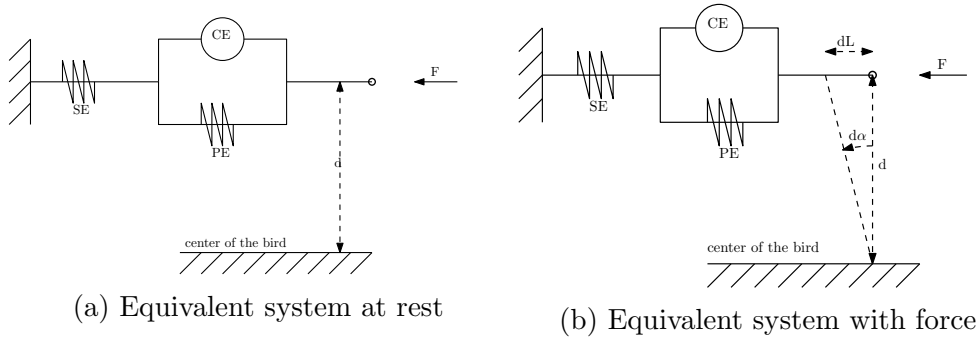


Figure 4.4: Equivalent system

The torque, T , applied on the rigid muscle can be expressed with an angle, $d\alpha$ and a angular stiffness, k_{ang} :

$$dT = k_{ang} \cdot d\alpha \Leftrightarrow k_{ang} = \frac{dT}{d\alpha} \quad (4.10)$$

The torque, T , is produced by the distance and the force.

$$T = d \cdot F \quad (4.11)$$

As illustrated on figure 4.4b and with the assumption that we are regarding the reaction of the system to a small force, we can approximate $\tan(d\alpha)$ by $d\alpha$.

$$d\alpha \cong \tan d\alpha = \frac{dL}{d} \quad (4.12)$$

Due to equation 4.11 and 4.12, the total angular stiffness of the system can be rewritten as:

$$k_{ang} = \frac{F \cdot d}{\frac{dL}{d}} = \frac{dF}{dL} \cdot d^2 \quad (4.13)$$

This equation is the general equation for the angular stiffness. Indeed, the system can experiment a contraction or an elongation, the angular stiffness will always keep this shape. It is the dF and dL that will change depending on the force applied on the system.

The change of length, dL , of the system is the sum of the deformation caused by the serie elastic element and the parallel elastic element. Also, the force in the serie elastic element, dF_{se} is equal to the total force of the system as mentioned with equation 4.2. And since we are in the case of a contraction, the force in the parallel elastic element, dF_{pe} , is equal to the difference between dF and the force of the contractile element, dF_{ce} , cf. equation 4.2.

$$\begin{aligned} dL &= dL_{se} + dL_{pe} \\ &= \frac{F}{k_{se}} + \frac{F - F_{ce}}{k_{pe}} \\ &= F \cdot \left(\frac{1}{k_{se}} + \frac{1}{k_{pe}} - \frac{F_{ce}}{F} \cdot \frac{1}{k_{pe}} \right) \end{aligned} \quad (4.14)$$

We can combine the expression of dL given by this equation in equation 4.13 in order to give a more defined expression of the angular stiffness.

$$k_{ang} = \frac{d^2}{\frac{1}{k_{se}} + \frac{1}{k_{pe}} - \frac{F_{ce}}{F} \cdot \frac{1}{k_{pe}}} \quad (4.15)$$

Equation 4.15 gives the final expression of the angular stiffness of the system. We notice that the angular stiffness depends on the stiffness of the serie elastic element, k_{se} and of the parallel elastic element, k_{pe} . The total force applied to the system also plays a role in the equation of the angular stiffness.

In the case of an elongation, the force, dF , is directed in the opposite direction on figure 4.4b. In this case, the change of length, dL , should not depend on the force of the contractile element, dF_{ce} . Indeed, the active element does not generate a torque when it is stretched (equation 4.9). The force of the parallel elastic element is equal to the force acting on the system. So equation 4.14 becomes:

$$\begin{aligned} dL &= \frac{dF}{k_{se}} + \frac{dF}{k_{pe}} \\ &= dF \cdot \left(\frac{1}{k_{se}} + \frac{1}{k_{pe}} \right) \end{aligned} \quad (4.16)$$

The angular stiffness of a system that undergoes an elongation, is defined as:

$$k_{ang} = \frac{d^2}{\frac{1}{k_{se}} + \frac{1}{k_{pe}}} \quad (4.17)$$

We notice that in this particular case the angular stiffness does not depend on the force acting on the system, i.e. it is linear.

The angular stiffness of the serie elastic element and parallel elastic element can then be found with a proportional factor:

$$\begin{aligned} k_{ang,se} &= k_{ang} \cdot \frac{k_{se}}{k_{se} + k_{pe}} \\ k_{ang,pe} &= k_{ang} \cdot \frac{k_{pe}}{k_{se} + k_{pe}} \end{aligned} \quad (4.18)$$

The angle at rest, θ_0 , can be defined with the behavior of the pectoralis muscle. Indeed, the pectoralis muscle contracts during the down stroke and elongates during the up stroke. So, the resting angle of the contractile element has to be near the maximum wing's angle value. Thus, the contractile element shortens during the down stroke and elongates during the upstroke [26].

$$\begin{aligned} \theta_{ce,0} &= 0.9 \cdot \theta_{max} \\ \theta_{se,0} &= 0.1 \cdot \theta_{max} \end{aligned} \quad (4.19)$$

4.3 Results

4.3.1 Linear muscle model

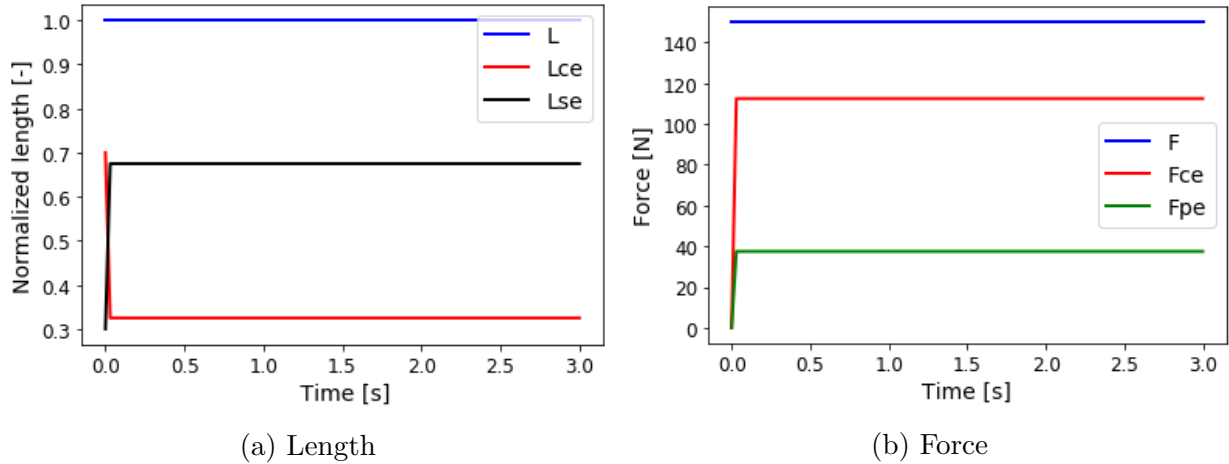


Figure 4.5: Evolution of the length and force of the different elements of a muscle model due to a constant total length, L , when a constant force is applied to the system

Figure 4.5 shows the reaction of the elements of the system when a constant force of 150 [N] is applied on the system. In this case, we fix the length at the beginning of the simulation and we observe how the elements react. This can be seen as a clamping experiment. The

value of the parameters used in this simulation are given in table 4.1. On figure 4.5a, we notice that the contractile element (red line) and serie elastic element (black line) do not stay in their original position. At the beginning, $L_{ce} = 0.7 \cdot L$ and $L_{se} = 0.3 \cdot L$. The active element contracts at the beginning and it stabilizes around its equilibrium length: $L_{ce,eq} = 0.3625 \cdot L$. On the other hand, at the beginning of the simulation, L_{se} appears to be stretched. It is the reason why its length increases before reaching its equilibrium length, $L_{se,eq} = 0.6375 \cdot L$. Figure 4.5b shows the evolution of the force of the different elements due to a constant force. We see that F_{ce} needs to generate a greater force than F_{pe} . In fact, $F_{pe} = \frac{k_{pe}}{k_{se}} F$ only when we fix the total length of the system constant. The force of the elements depends on the stiffness of the 2 elastic elements.

Constant	Value [N/m]
$k_{se,lin}$	400
$k_{pe,lin}$	100

Table 4.1: Value for the stiffness of the elastic elements

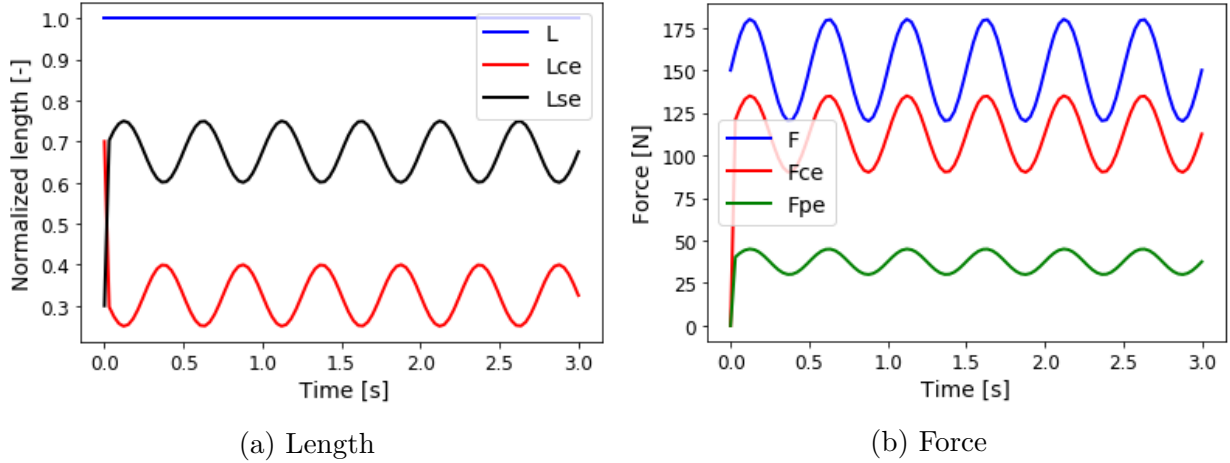


Figure 4.6: Evolution of the length and force of the different elements of a muscle model due to a fixed constant total length, L , when an oscillating force is applied to the system, $F = (\sin(2\pi t \cdot 2) \cdot 0.2 + 1) \cdot 150$

Figure 4.6 shows the evolution of the length and force of the element when we keep the system at a constant length and apply an oscillating force on it (same average value as for the simulation on figure 4.5b). Indeed, in the daily life, the force applied to a muscle can vary. We notice that L_{ce} and L_{se} now are oscillating. However, they oscillate around their equilibrium length shown in figure 4.5. F_{pe} is still equal to $\frac{k_{pe}}{k_{se}} F$ even though the force is now oscillating.

The length of a muscle does not have to stay constant. It can contract, or elongate as well which leads to a variation of the muscle's length. Figure 4.7 shows the reaction of the

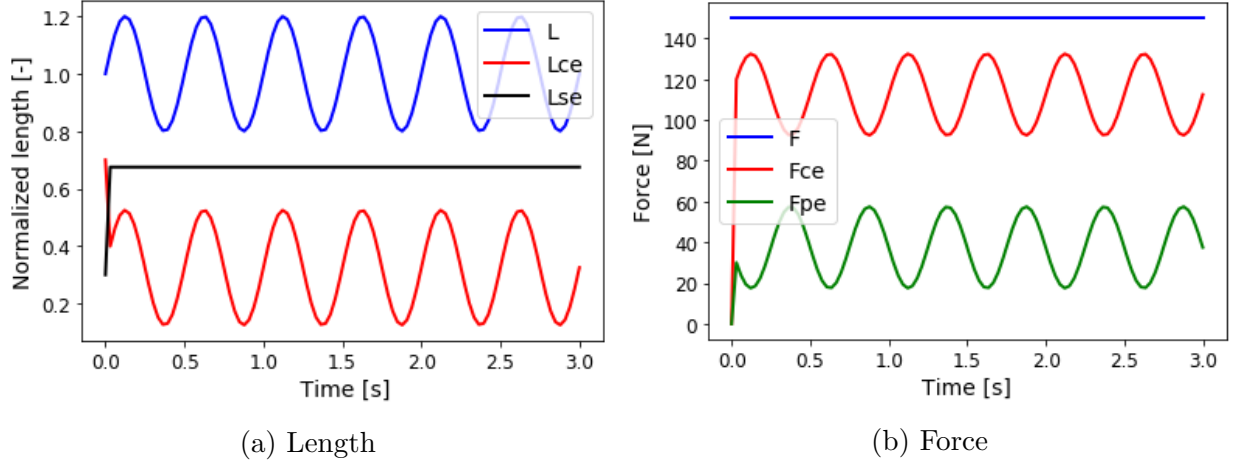


Figure 4.7: Evolution of the length and force of the different elements of a muscle model due to an oscillating total length, $L = \sin(2\pi t \cdot 2) \cdot 0.2 + 1$ when a constant force is applied to the system

length and force of the elements when a constant force is applied and figure 4.8 shows the reaction of the element's length and force when an oscillating load is applied. In the first case, we notice that the length of the serie elastic element stays constant, only the contractile element's length oscillates. This is due to the fact that $F_{se} = F$ which is fixed constant. In figure 4.8, we see that all the lengths oscillate when the applied force varies. In this case, $F_{pe} \neq \frac{k_{pe}}{k_{se}} \cdot F$

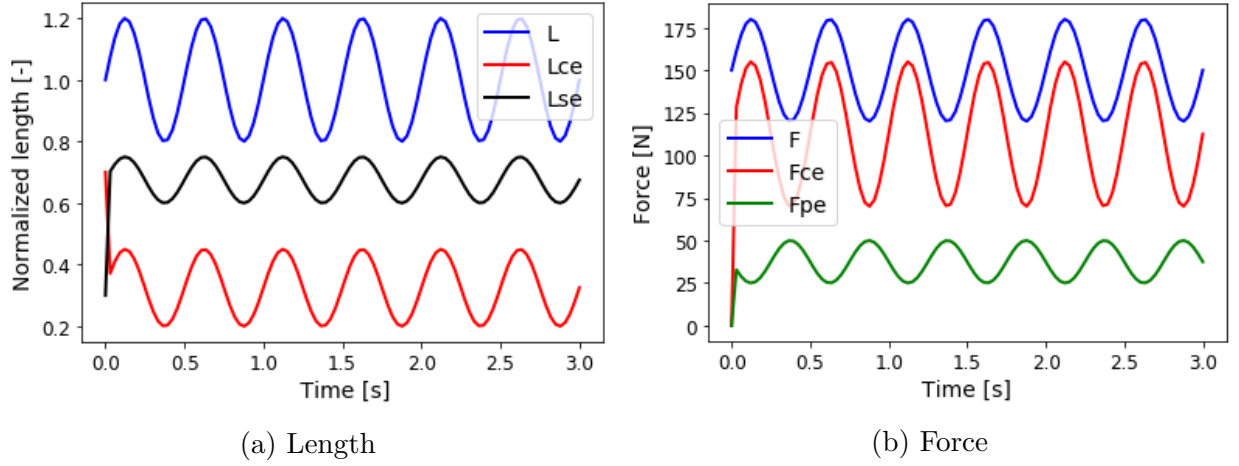
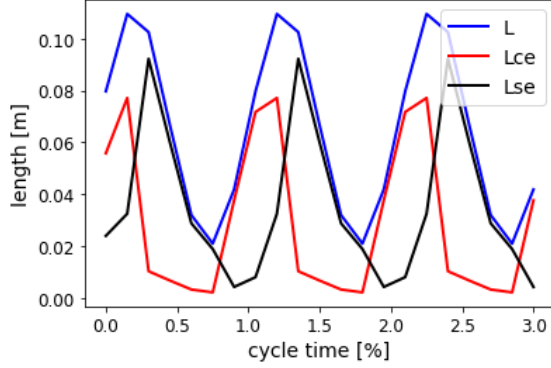
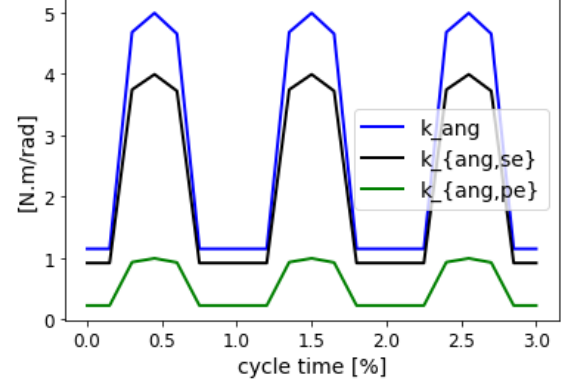


Figure 4.8: Evolution of the length and force of the different elements of a muscle model due to an oscillating total length, $L = \sin(2\pi t \cdot 2) \cdot 0.2 + 1$ when an oscillating force is applied to the system $F = (\sin(2\pi t \cdot 2) \cdot 0.2 + 1) \cdot 150$

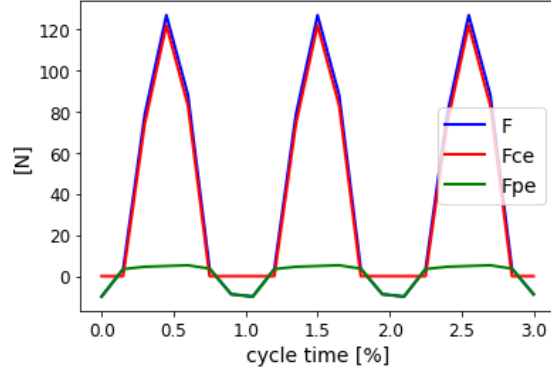
4.3.2 Equivalent system



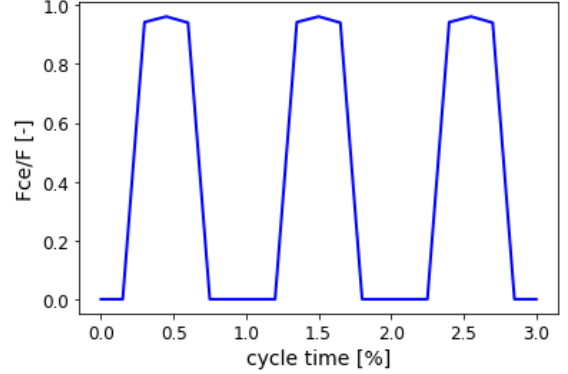
(a) Evolution of the length of the equivalent system



(b) Evolution of the angular stiffness of the equivalent system



(c) Evolution of the force of the equivalent system



(d) Evolution of F_{ce}/F of the equivalent system

Figure 4.9: Equivalent system for a bird flying at a speed of 15 [m/s] and frequency of 4 [Hz]

Now that we understand how a linear muscle model works, we can move on to the analysis of the equivalent system in order to compute the angular stiffness of the angular muscle model. In section 4.2.1, I developed the equivalent model. From equation 4.15, we notice that k_{ang} depends on the linear stiffness k_{se} and k_{pe} , on the ratio $\frac{F_{ce}}{F}$ and the length of the pectoralis muscle.

First we need to determine the length of the pectoralis muscle. The length of pectoralis fibers of the common pigeon lays between 31 and 67 [mm] [14]. During the writing of this thesis, I study the behavior of the bald ibis. The length of the pectoralis muscle does change from species to species. To adapt this length to the bald ibis, the ratio of their respective wingspan is needed.

$$\frac{l_{pigeon}}{l_{ibis}} = \frac{wingspan_{pigeon}}{wingspan_{ibis}} \Leftrightarrow l_{ibis} = l_{pigeon} \cdot \frac{wingspan_{ibis}}{wingspan_{pigeon}} \quad (4.20)$$

The bald ibis has a wingspan of 1.2 [m] and the pigeon of 0.670 [m] [27]. So the length of

the pectoralis muscle of the bald ibis is equal to 0.12 [m]. This refers to the distance, d , of the equivalent system.

F and dL are obtained from the aerodynamics. Since the aerodynamic gives the motion of the wing, θ and the torque applied by the wing on the center of the bird, T , finding F and dL is straightforward. We have to take the reciprocal equation of equation [4.11](#) and [4.12](#).

$$F = \frac{T}{d} \quad (4.21)$$

$$dL = d \cdot \tan(d\theta) \quad (4.22)$$

Figure [4.9](#) shows the evolution of the length, force, angular stiffness and ratio of $\frac{F_{ce}}{F}$ of the different elements of the equivalent system. We notice that the angular stiffness of the system and also of the serie and parallel elastic elements are time-dependent and non-linear (figure [4.9b](#)). $k_{ang,se}$ varies from 0.92 to 3.99 [N.m/rad]. On the other hand, $k_{ang,pe}$ is smaller and varies from 0.23 to 1.00 [N.m/rad]. This is due to the fact that the linear stiffness of the serie elastic element is bigger than the one of the parallel elastic element, 400 [N/m] vs 100 [N/m].

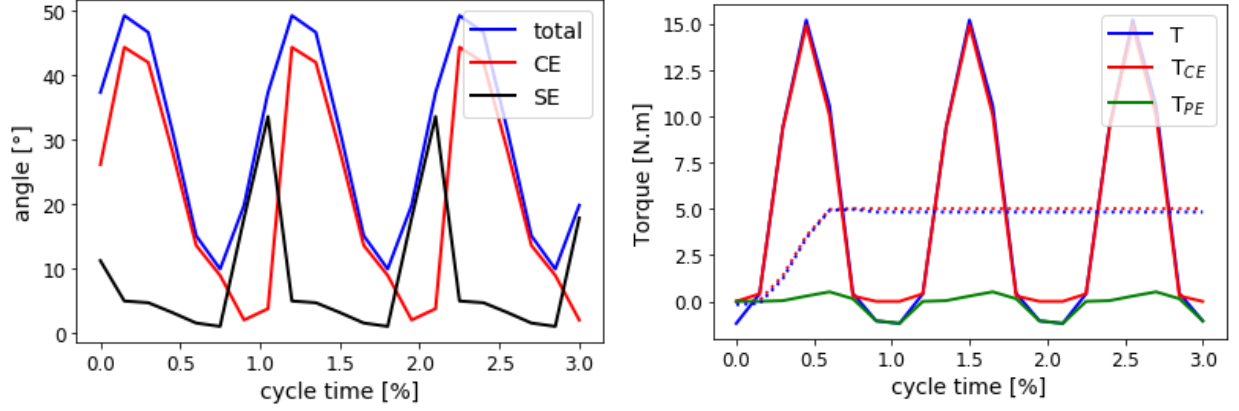
From figure [4.9c](#), we see clearly that F_{ce} is bigger than F_{pe} when the contractile element is in contraction, i.e. during the downstroke. In this case, F_{ce} varies from 0.94 to 0.96 times F as it is illustrated in figure [4.9d](#). However, when the contractile element is no longer in contraction, F_{ce} drops to 0. Hence, the ratio $\frac{F_{ce}}{F}$ drops also to 0 in this case. This shows that in upstroke the sarcomeres do not carry out any work and the movement is passive.

4.3.3 Angular muscle model

Now that we have a value for the angular stiffness of the serie and parallel elastic element, it is possible to analyze the angular muscle model for a bird. This angular model takes in input the kinematics of the wing and the dynamics of the wing (torque applied by the wing on the center of mass). The angle on figure [4.10a](#) is formed by its wing and a horizontal line passing through the center of mass. To this value, twice the minimum value of the angle is add in order to have the motion of the wing and an angle that is always positive. The blue line represents the wing's angle in figure [4.10a](#) and the blue line represents the wing's torque in figure [4.10b](#) for a speed of 14 [m/s] and a wingbeat frequency of 4 [Hz]. I used to investigate the angular model because bald ibis fly at an average speed of 14 [m/s].

Figure [4.10a](#) shows the reaction of the contractile element's angle (in red) and the serie elastic element's angle (in black). θ_{ce} and θ_{se} vary strongly but have a periodic behavior. These angles cannot be smaller than 10% of the total angle and bigger than 90% of the total angle because the elastic elements have a finite length. We notice that during the downstroke, when θ decreases, θ_{ce} decreases and consequently θ_{se} increases. This means that the contractile element contracts during this period. On the opposite during the upstroke, θ_{ce} increases and consequently θ_{se} decreases.

Figure [4.10b](#) shows the evolution of T_{ce} (in red) and T_{pe} (in green). As a reminder, the down stroke is the power stroke while the up stroke is called the recovery stroke. We notice



(a) Evolution of the angles for a oscillating total angle (b) Evolution of the torque of the different elements

Figure 4.10: Evolution of the angle and torque of CE, PEE and SEE for a bald ibis flying at a speed of 14 [m/s] with a wingbeat frequency of 4[Hz].

that during the down stroke, the total torque increases. T_{ce} follows this behavior. Its torque increases while it is contracted until θ reaches its maximum value. Then T_{ce} decreases during the up stroke. We also notice that T_{pe} is way smaller than T_{ce} . This is the results of the low stiffness of the parallel elastic element. The contractile element contributes up to 98% of the total torque applied to the model. This shows that the contractile element is the major component during the down stroke.

The dotted line represents the average value during 1 period of the contractile element's torque, in red, and the average value during 1 period of the wing's torque, in blue. For a velocity of 14 [m/s], $T_{avg} = 4.82$ [N.m] and $T_{ce,avg} = 5.00$ [N.m]. $T_{ce,avg}$ is bigger than T_{avg} because the bird's torque presents negative values and the contractile element cannot generate a negative torque.

4.3.4 T_{ce} -velocity relationship

In this section, the influence of the velocity on the torque of the contractile element is analyzed. The $T_{ce,avg}$ -velocity and power-velocity relationships have not the same profile. Figure 4.11 presents a plateau for small velocities. For velocities higher than 13 [m/s], the average contractile torque increases rapidly. This is not a U-shaped curve like it is explained with figure 2.5a. The $T_{ce,avg}$ -velocity relationship does not present a minimum value. When the speed decreases below 13 [m/s], the torque decreases slightly.

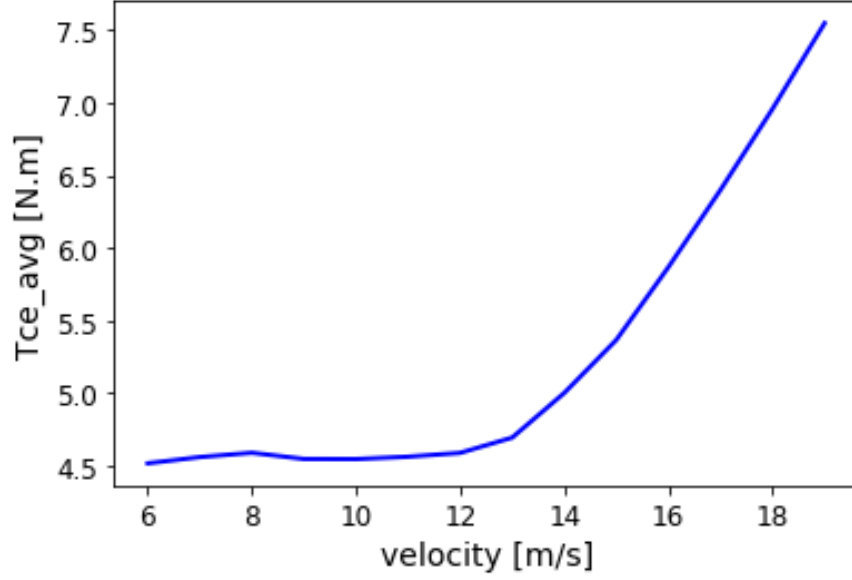


Figure 4.11: Evolution $T_{ce,avg}$ as a function of the bird's speed

4.4 Conclusion

The contraction of skeletal muscles can be schematized with a contractile element, CE, and 2 elastic elements, one placed in parallel to CE, called PEE, and one placed in serie to CE and PEE, called SEE. This muscle model can reproduce the kinematics and dynamics of a bird. It takes the torque of the wing applied to the center of the bird and the wing's angle as input and it gives the evolution of the angle of the contractile element and serie elastic element as output. It also shows the evolution of the distribution of the torque in the contractile and parallel elements. The model works for a large range of velocities and wingbeat frequencies. The reaction of the torque generated by the contractile element will be of interest when the aerodynamic and fatigue models will be combined.

Chapter 5

Combined model

The final goal of this thesis is to understand and analyze the fatigue phenomenon on birds in order to find which parameters have an influence on the endurance time, or the total distance travelled.

This chapter starts with an explanation on how to couple the fatigue model with the muscle model and the aerodynamics of a bird. The models used here are explained and analyzed in the previous chapters. As the different constants in the model must be chosen wisely, the choice process will be explained. Finally, general results will be shown and then the impact of the parameters will be explained. The results on one bird is firstly described. Then a second bird is added in order to analyze and see the benefits of the follower by flying in the upwash region of the leader. The velocity and the distance will be analyzed. Relationships between these parameters and the endurance time will follow, and conclusions will be taken.

5.1 Methodology

5.1.1 Link between aerodynamics and muscle model

The muscle model has 2 inputs: the total angle, θ and the total torque applied to the model, T_{bird} . This gives in output the angle of the different elements, θ_{se} and θ_{ce} , and the torque on the active element, T_{ce} as well as the torque of the parallel elastic element, T_{pe} .

The aerodynamics model of the bird gives the motion of the wing so that the total angle can be directly derived from it. It also gives the torque of the wings on the center of the bird. This torque is defined as, T_{bird} . It will be used to determine the torque of the contractile elements.

The muscle model explained in Chapter 4 is able to generate a torque in one direction only. So in order to simulate a bird, 2 muscle models are needed, one per wing. The muscle model is composed of one contractile element, CE, in parallel with an elastic element, denoted PE. These 2 elements are in serie with an other elastic element, denoted SE. Figure 5.1 is a schematic representation of a bird. The first model generates a torque on the left wing and the second on the right wing. We notice that in this configuration, the muscle models are located below the wings which is also the case for the bird's muscles. This special feature provides active muscular torque in downstroke, when most of the flight efforts are concentrated.

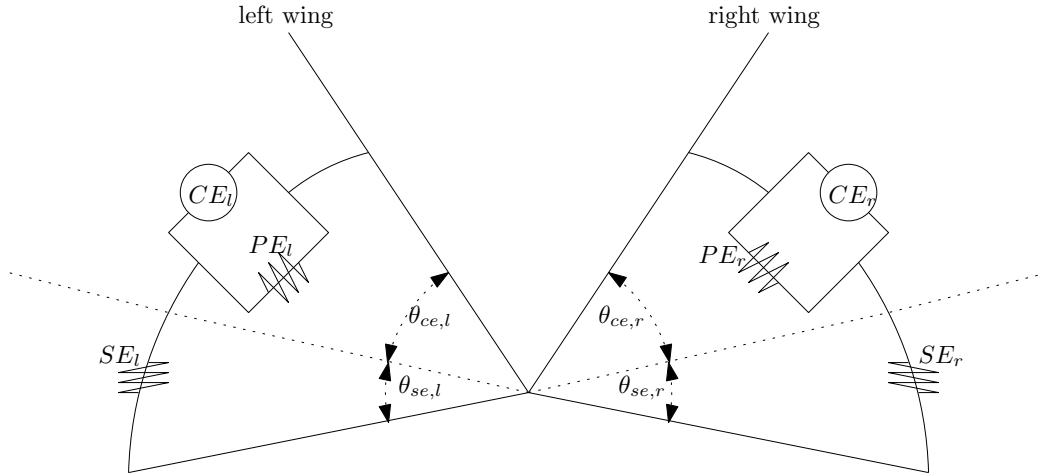


Figure 5.1: Schematic representation of a bird's muscle models

Since the motion of the 2 wings are assumed to be identical, the wing's angles are the same at every time step.

$$\theta = \theta_l = \theta_r \quad (5.1)$$

The internal torque of the wings on the center of the bird is divided into the 2 muscle models. For a single bird and a leader, since we assumed that the bird is symmetrical, the torque applied by the left wing is the same as the torque applied by the right wing.

$$T_{bird} = T_l + T_r \Leftrightarrow T_l = T_r = \frac{T_{bird}}{2} \quad (5.2)$$

However, it is not the case anymore when we simulate the interaction between multiple birds. The follower saves power when it flies behind the leader. So, the torque applied by the 2 wings on the center of the bird is not the same anymore. When flying in a v-shaped formation, only one of the two follower's wing can benefit of the upwash region. On figure 5.2, birds on the left of the leader reduce their induced power of their right wing while birds on the right reduce their induced power of their left wing. For the purpose of this study, we will focus on the left-leg of the flock. The left wing does not take advantage of the upwash created by the bird in front of him, only the right wing can take advantage of it.

$$\begin{aligned} T_1 &= T_{leftwing} \\ T_2 &= T_{rightwing} \end{aligned} \quad (5.3)$$

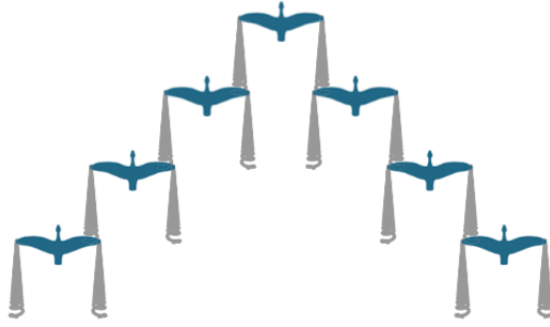


Figure 5.2: V-shaped formation

As a reminder, here is how to determine the active torque of the muscle model at every time-step.

$$\begin{aligned} \theta &= \theta_{se} + \theta_{ce} \\ T_{wing} &= T_{se} = T_{ce} + T_{pe} \end{aligned} \quad (5.4)$$

With these 2 equations and the fact that the serie element is elastic, θ_{se} , θ_{ce} and T_{ce} can be derived:

$$\theta_{se} = \theta_{se,0} + \frac{T_{bird}}{k_{se}} \quad (5.5)$$

$$T_{ce} = T_{bird} - k_{pe} \cdot (\theta_{ce,0} - \theta_{ce}) \text{ where } \theta_{ce} = \theta - \theta_{se} \quad (5.6)$$

A muscle model has 3 parameters that need to be determined :

- the angular stiffness of the parallel elastic element, k_{pe}
- the angular stiffness of the serie elastic element, k_{se}
- the equilibrium angle, θ_0

Since the wing are symmetrical, the parameters of the muscle models are identical. The 2 wings are composed of the same muscle. They are designed in the same way.

5.1.2 Link between muscle model and fatigue model

The fatigue model explained in Chapter 3 has only 1 input: the target load. The target load is defined as:

$$TL = \frac{F_{current}}{F_{max}} \quad (5.7)$$

In our case, the contractile elements of the models represent the active behavior of a muscle. So only these experience the fatigue phenomenon since the elastic elements are passive. The link between the fatigue model and the muscle model lays in the definition of the target load. The target load of a bird can be defined as the ratio of the active torque and the maximal torque of the active element.

$$TL(t) = \frac{T_{ce}(t)}{T_{ce,max}} \quad (5.8)$$

$T_{ce,max}$ is a constant. This value will influence the intensity of the target load so it needs to be defined wisely since specific experimental data are absent. We just need to choose the right value for the fatigue and recovery coefficients, F and R. Once reasonable coefficients and $T_{ce,max}$ are determined, we can analyze the evolution of the activated muscle states, M_a , fatigued muscle states, M_f and resting muscle states, M_r , in order to evaluate the endurance time.

5.1.3 Choice of constants

We now need to determine the constants according the aerodynamics of the bird. The fatigue model has 3 constants:

- recovery coefficient, R
- fatigue coefficient, F
- the maximal torque of the contractile element, $T_{ce,max}$

The Hill's muscle model has 3 parameters as well:

- stiffness of the parallel elastic element, k_{PE}
- stiffness of the serie elastic element, k_{SE}
- angle at rest, θ_{opt}

The target load derived from the active element is not constant but dynamic. Indeed, T_{ce} varies with the kinematic of the wing. However, from figure [3.7](#), we know that the frequency of the target load does not impact the endurance time for frequencies in the range of 2 [Hz] to 12 [Hz]. This is the case only if the fatigue and recovery coefficients are small enough compared to the frequency. In the literature, we cannot find value of F and R for birds. So I choose to take the value of F and R that are present in the human shoulder joint region of human [\[20\]](#). I choose them because the shoulder is the joint region that behaves the most like a bird's wing.

$$F = 0.01820[Hz]$$

$$R = 0.00162[Hz]$$

F and R are respectively, 100 and 1000 times smaller than the frequency so we can assume that TL depends only on its average value and not on its frequency.

We now need to determine $T_{ce,max}$ in order to fix all the constants of the fatigue model. We remember that the endurance time increases when the intensity of the target load decreases as it is illustrated on figure 3.4. Also on this figure, we know that if $TL < \frac{1}{\frac{F}{R}+1}$, then the muscle unit does not get tired at all. So the target load has to be as close as possible to the asymptotic value in order to have a high ET. In other words, we can choose to fix the endurance time and for this ET, choose the right value of TL by adding a small value, $\delta(TL)$ in order to match the target load to the endurance time:

$$TL = \frac{1}{\frac{F}{R} + 1} + \delta(TL) \quad (5.9)$$

Once we have the value of TL, we can finally find a suitable value for $T_{ce,max}$.

$$TL = \frac{T_{ce,avg}}{T_{ce,max}} \Leftrightarrow T_{ce,max} = \frac{T_{ce,avg}}{TL} \quad (5.10)$$

In this equation, $T_{ce,avg}$ is the average value of the torque that the contractile element has to generate. TL can also be replaced by equation 5.9. Thus it depends only on $\delta(TL)$, $T_{ce,avg}$, F and R. $T_{ce,max}$ is here found theoretically because there are no experimental data of this parameters.

The value of T_{ce} varies with the endurance time and also with the bird's velocity, cf. figure 4.11. A benchmark value needs to be determined. Due to this value, the impact of the velocity on the endurance time can be analyzed. $T_{ce,max}$ is taken from a bald ibis, bird of interest in this work, flying at a speed of 13 [m/s]. This velocity is chosen because it is the velocity at which the bird's range is maximal, as it is shown on figure 2.5a. The wingbeat frequency is of 4 [Hz] because bald ibises mostly move their wings at this frequency, cf. table 2.1.

In the case of a simulation with multiple birds, the value of $T_{ce,max}$ stays constant for all the birds composing the flock. The constant value is the one inferred for the leader.

Regarding the angular stiffness, the way to obtain it is explained in Chapter 4. With the use of an equivalent system that takes the kinematics and dynamics of a bird's wing as input, $k_{se,ang}$ and $k_{pe,ang}$ can be totally defined. These values can be adjusted when the speed or wingbeat frequency change.

The last parameter that needs to be defined is θ_0 . Since the contractile element has to generate a torque during the downstroke, θ_0 needs to be in the region of the maximal value

of the wing's angle.

$$\begin{aligned}\theta_{ce,0} &= 0.9 \cdot \theta_{max} \\ \theta_{se,0} &= 0.1 \cdot \theta_{max}\end{aligned}\tag{5.11}$$

This values ensure that the contractile element contracts and generates a torque during the downstroke [26].

5.2 Results

5.2.1 Solo flight

Figure 5.3 combines the aerodynamics of a bird with a muscle model. The endurance time is then obtained with the fatigue model that takes the evolution of T_{ce} with time as input. Figure 5.3a shows the reaction of θ_{ce} and θ_{se} in order to reproduce the kinematics and dynamics of the wing. We notice that θ_{ce} decreases during the down stroke (when the total angle decreases). During this period, the contractile element is contracted. Therefore, T_{ce} increases during this stroke as we can see on figure 5.3b. For this simulation, the speed is taken equal to 13 [m/s]. At this specific velocity, the bird's range is maximal. The bird is assumed to fly during 2 hours without getting fatigued, ET=2 hours. This means that the bird is able to cover a distance of 94 km before feeling fatigued. Table 5.1 indicates the value of the parameters in order to achieve an endurance time of 2 hours. We notice that $\delta(TL)$ is really small, 10^{-6} . Since the ET-relationship presents a kind of exponential behavior, a small added value to the target load results in a big change in endurance time, cf. figure 3.4

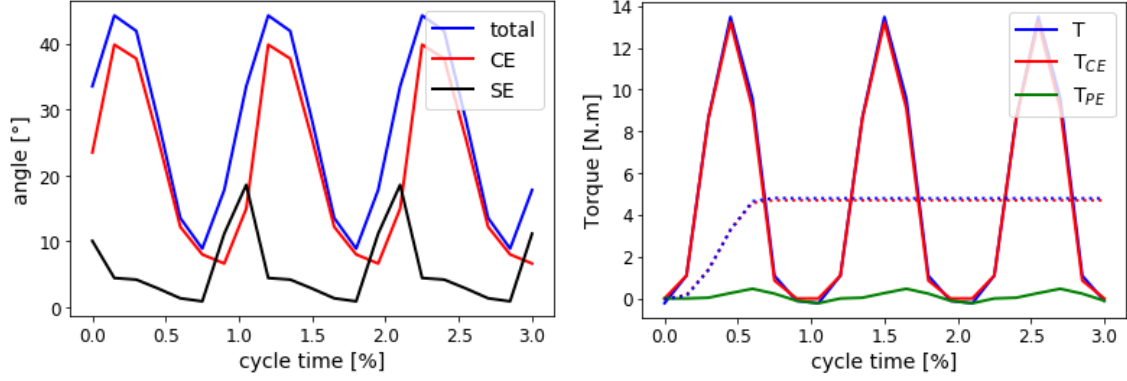
	ET=2 hours	ET=1h30	ET=1 hour
δTL [-]	10^{-6}	10^{-5}	$2 \cdot 10^{-4}$
TL [-]	0.08450804	0.08451704	0.08470704
$T_{ce,avg}$ [N.m]	4.6981	3.3601	3.3601
$T_{ce,max}$ [N.m]	55.5938	55.5879	55.4632

Table 5.1: Constant value for a bald ibis, v=13 [m/s] and freq=4 [Hz]

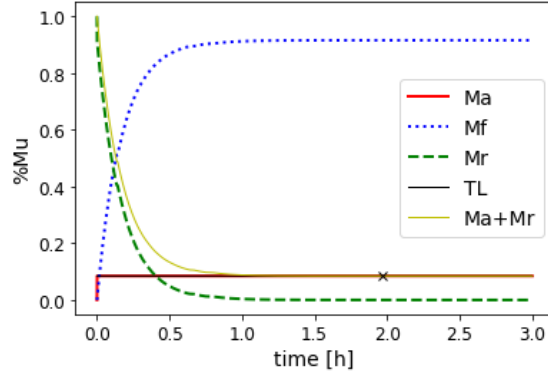
Table 5.1 shows the different values that $\delta(TL)$, TL, $T_{ce,avg}$ and $T_{ce,max}$ need to be equal to in order to obtain an endurance time of 2 hours, 1h30 and 1 hour. To pass from ET=2 hours to an ET of 1 hour, δTL is 200 times bigger but the respective value is really small. The difference in $T_{ce,max}$ is less consequent. Indeed, the value passes from 55.5938 to 55.4632 [N.m]. This is the result of the small variation of target load. However, this small variation leads to a big difference in terms of endurance time.

ET-velocity relationship

It is interesting to look at the impact of a bird's speed on the endurance time. The results shown in figure 5.4 are taken with respect to v=13 [m/s]. At this velocity, the endurance time is calculated to be equal to 2 hours.



(a) Angle evolution of the wing, CE and SE (b) Evolution of the torque of CE and PE. The dotted lines represent the average value of T (in blue) and T_{ce} (in red)



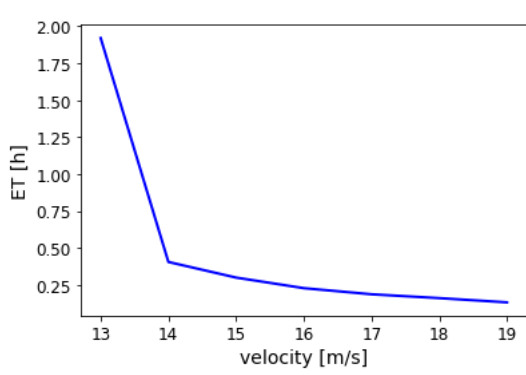
(c) Evolution of M_a , M_f and M_r . The cross indicates the endurance time

Figure 5.3: Endurance Time of a bald ibis, flying at a velocity of 13 [m/s] and wingbeat frequency of 4 [Hz]

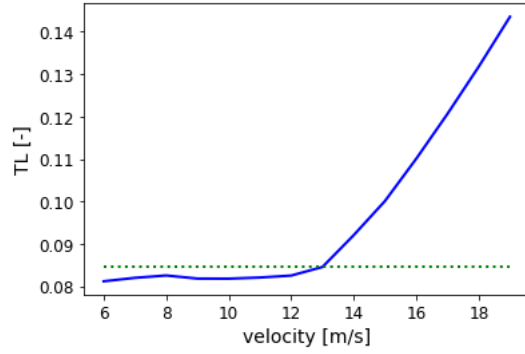
The first thing to notice is that the endurance time decreases abruptly for speed higher than 13 [m/s]. This is the result of the increasing average value of T_{ce} when the velocity increases, cf. figure 4.11. So the target load which is defined as the ratio of $T_{ce,avg}$ and $T_{ce,max}$ increases when the speed is higher than the benchmark speed. Figure 5.4b shows the specific behavior of TL with respect to the speed. For a speed of 13 [m/s], the endurance time is of 2 hours as predicted. However, for a speed of 14 [m/s], usual speed of a bald ibis during migration, the endurance time drops to 25 minutes.

The second thing to notice is that for velocities lower than 13 [m/s], the endurance time is infinite. This is also due to the fact that $T_{ce,avg}$ decreases when the speed drops. The target load falls below the asymptotic value of TL, see equation 3.5 because small changes of TL leads to big changes of endurance time. Figure 5.4b illustrates this particular behavior.

Figure 5.5 shows also the ET-speed relationship and TL-speed relationship but in this case, the bird's speed is of 9 [m/s]. This speed is the minimum power speed of the bald ibis, speed for which the required power is minimal. We notice that for a speed of 9 [m/s], the

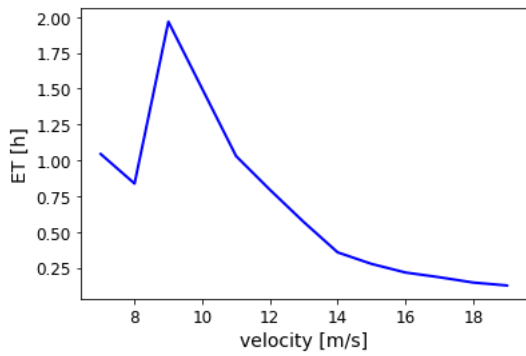


(a) Evolution of ET for different velocities

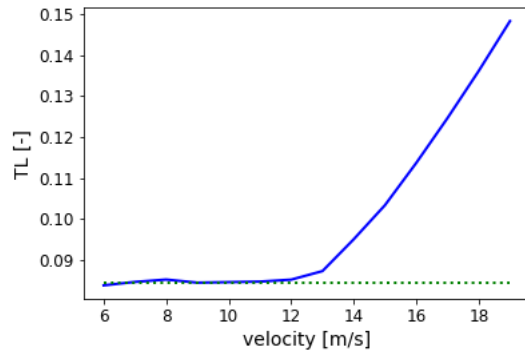


(b) TL for different velocities. The dotted line represents the asymptotic value of M_a

Figure 5.4: Evolution of the endurance time and target load with $T_{ce,max}$ taken for a speed of 13 [m/s]



(a) Evolution of ET for different velocities



(b) TL for different velocities. The dotted line represents the asymptotic value of M_a

Figure 5.5: Evolution of the endurance time and target load with $T_{ce,max}$ taken for a speed of 9 [m/s]

endurance time is 2 hours. For higher velocities, the endurance time decreases less abruptly than on figure 5.4. However, for the 2 benchmark velocities, the 2 endurance times converge towards the same value. Indeed, for large velocities, the target load increases. When the intensity of the target load increases, the impact on the endurance time is less important than for low intensities. When we look at figure 5.5b and figure 5.4b, we notice that the target loads tend to the same value. The main difference between figure 5.5a and figure 5.4a is that for a benchmark velocity of 9 [m/s], the endurance time is not infinite for a speed of 7 and 8 [m/s], it has an endurance time of, respectively, 1 hour and 48 minutes. It is due to the variation of $T_{ce,avg}$. Figure 4.11 shows the relation between the average contractile torque and velocity. In fact, for speed below 9 [m/s], $T_{ce,avg}$ increases a little. This increase creates a small increase of the target load that leads to a smaller endurance time.

5.2.2 Tandem flight

In this section, the different behavior between leader and follower is discussed. When birds fly in a flock, they mostly swap positions between pairs [12]. Therefore, I focus on a tandem flight, on the interaction of 2 birds, a leader and a follower. As we remember from Chapter 2, when the follower takes advantage of the upwash created by the leader, power can be saved. This saved power depends on the velocity and the relative position of the follower compared to the leader. The conclusion was that for a speed of 13[m/s] (maximum range speed), the follower needs to be placed 2 [m] behind the leader and their wingtips must overlap over a distance of 0.13 times their wingspan.

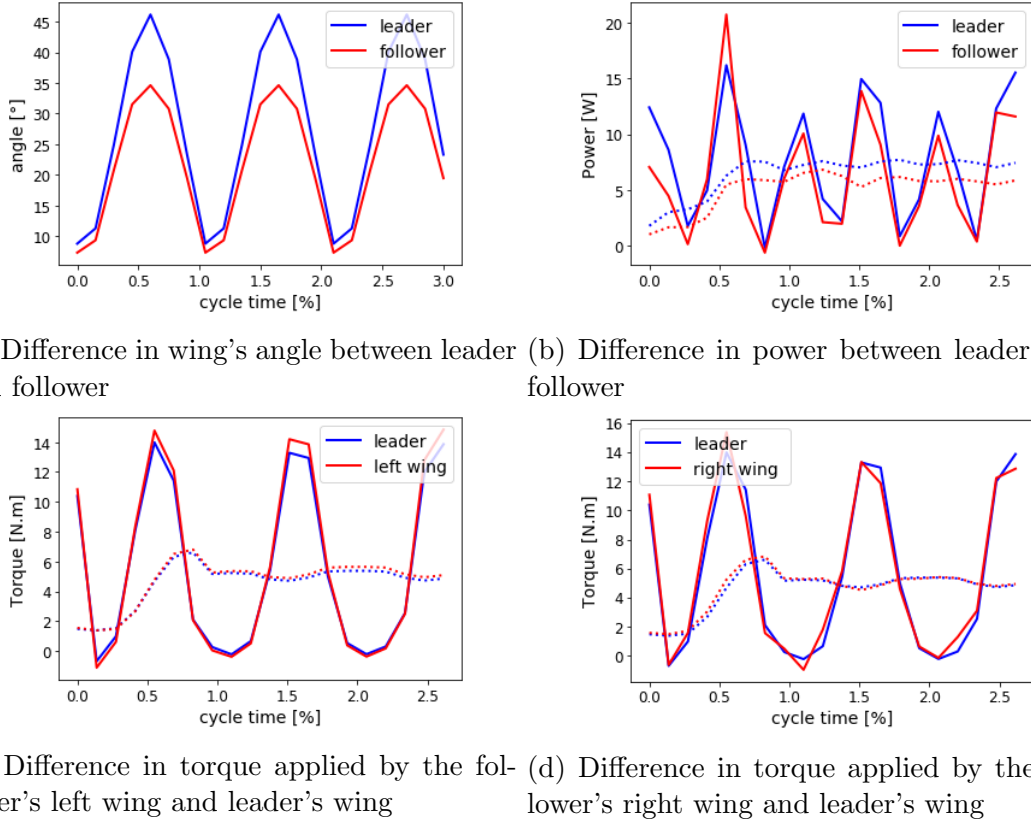


Figure 5.6: Tandem flight of bald ibis, speed=13 [m/s]. The dotted lines represent the average value of the respective plain line.

This section focuses on the difference in the internal torque and angle between leader, follower's left wing and follower's right wing, as it is shown on figure 5.6. We focus only on one wing of the leader as they undergo the same motion and forces. However, since the follower is placed behind the leader, the force acting on the follower's wings are not the same anymore. This is the reason why we have to investigate the behavior of the 2 wings of the follower. In the simulation, the follower is placed to the left of the leader, cf. left leg of a v-shaped formation on figure 5.2. So, the left wing does not take advantage of the upwash region while the right wing does take advantage.

Figure 5.6a shows the difference of wing's angle between leader and follower. The left and right wing of the follower undergo the same motion so the wing's angle does not change between the 2 wings. It is only the forces acting on the wings that change. We see that the amplitude of the leader's wing is bigger than the amplitude of the follower's wing. The maximum difference is in the range of 11° .

When we look at the torque applied by the wing on the center of the bird, we notice that the leader's torque is smaller than the follower's left and follower's right wing, see figure 5.6c and figure 5.6d. However, the difference is small as it is shown in table 5.2. We also notice that the left wing needs to develop more torque compare to the right wing.

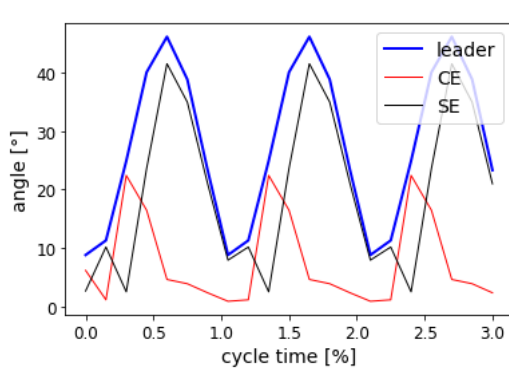
	T_{avg}	$T_{ce,avg}$	$T_{ce,max}$
Leader	4.8587 [N.m]	4.6692 [N.m]	55.2515 [N.m]
Follower's left	5.0863 [N.m]	5.0135 [N.m]	55.2515 [N.m]
Follower's right	4.9422 [N.m]	4.7917 [N.m]	55.2515 [N.m]

Table 5.2: Average values of the total torque applied on the center of the bird and the contractile element's torque

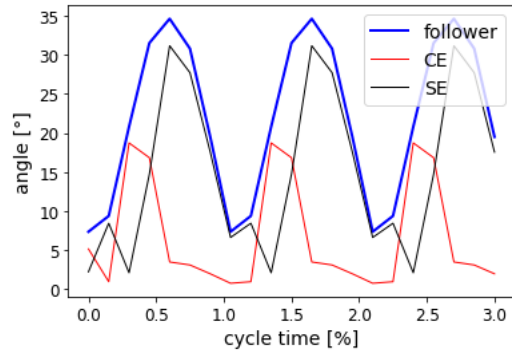
We remember from the aerodynamic chapter that the follower reduces its power by flying in the upwash region. Figure 5.6b illustrates this behavior for a velocity of 13 [m/s]. The difference of power comes mostly from the difference of wing amplitude than from difference of torque.

Figure 5.7 shows the evolution of the muscle model of the follower's left and right wing and one of the leader's wing. Figure 5.7a and figure 5.7b illustrate the evolution of the angle the contractile element and serie elastic element for the leader and follower. When the total wing's angle increases, θ_{ce} increases. It is the upstroke. When the total wing's angles decreases, θ_{ce} shortens. It is the down stroke. When the contractile element is contracted, a torque is generated as we can see on figure 5.7e, figure 5.7g and figure 5.7c. We notice that on these 3 figures, T_{ce} is activated/generates a torque during the down stroke. During the upstroke, T_{ce} decreases and becomes equal to 0 [N.m]. It is the recovery stroke.

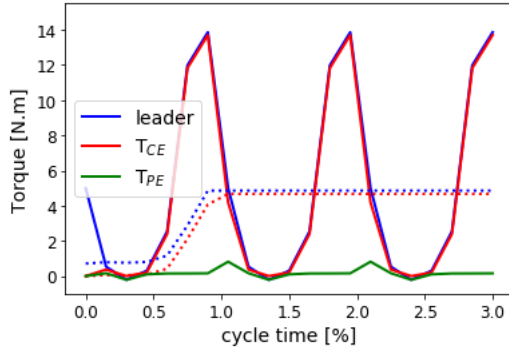
From $T_{ce,avg}$, it is possible to obtain the endurance time of the wing. In order to compute the endurance time of the follower, the value of $T_{ce,max}$ is taken from the leader as it is explained in section 5.1.3. The endurance time of the leader is 2 hours (1h58 exactly). However, the endurance times of follower's wings are less important. The left wing can work during 28 minutes before feeling fatigued and the right wing can work during 38 minutes. We see that the upwash has a positive effect on the endurance time between the 2 wings because the right wing could work 10 more minutes compared to the left wing. Hence, the endurance time of the follower is equal to the minimum ET of the 2 wings, $ET_{follower}=28$ minutes. This value is really small compared to ET_{leader} . The follower can fly over a distance of 21.8 [km] while the distance covered by the leader is 92.2 [km]. The follower can fly less than 25 % of the leader's distance.



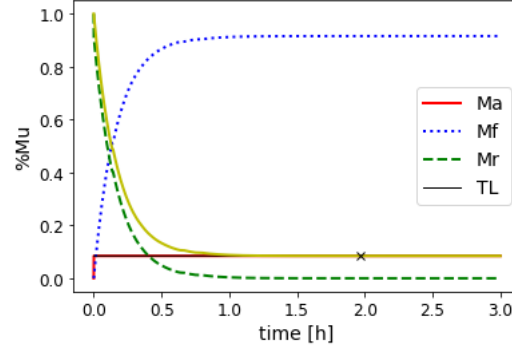
(a) Evolution of θ_{ce} and θ_{se} of the leader



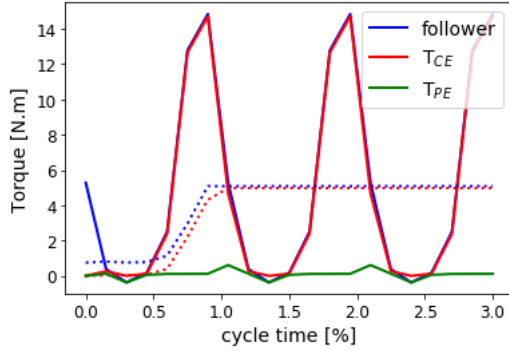
(b) Evolution of θ_{ce} and θ_{se} of the follower



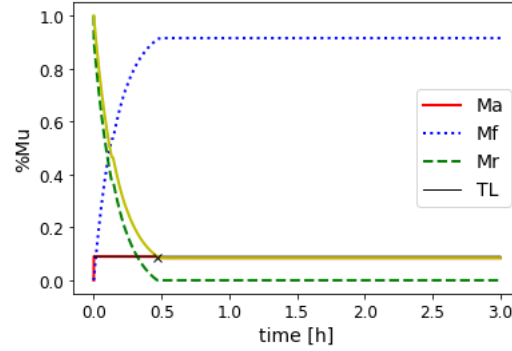
(c) Evolution of T_{ce} and T_{pe} of the leader



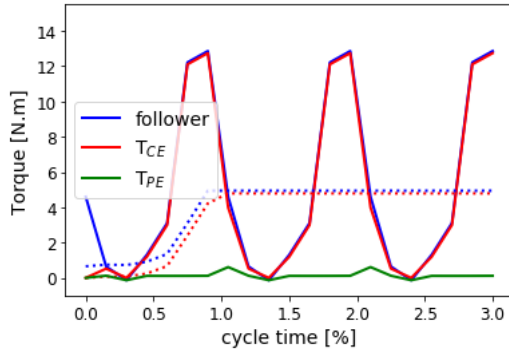
(d) Evolution of the muscle states of the leader.



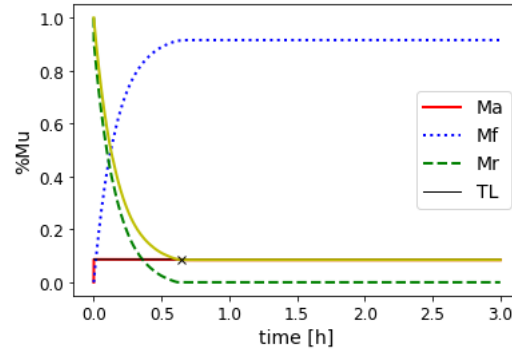
(e) Evolution of T_{ce} and T_{pe} of the follower's left wing



(f) Evolution of the muscle states of the follower's left wing.



(g) Evolution of T_{ce} and T_{pe} of the follower's right wing



(h) Evolution of the muscle states of the follower's right wing.

Figure 5.7: Comparison of the results between the leader and follower. Parameters: $v=13$ [m/s], wingbeat frequency=4[Hz], depth=2[m], wingtip spacing=0.13·wingspan

5.3 Conclusion

This shows that, during collective migratory flight, this particular muscle fatigue model does not predict swaps aimed at sharing the fatigue-related load of being leader. Besides, these results might be more general than the particular models used in this thesis. It was indeed already suggested by B. Vloelkl and S. Portugal [12] that: "if muscle fatigue is the leading mechanism of position swaps during collective bird migration, we should expect that leading time should decrease with time as birds should tire and that the average time in the leading position should be correlated with the strength of the birds. However, no such data have been recorded.". This last sentence finds further validation in my computations. In fact the endurance time of followers in favorable positions is reduced, whereas considerable energy savings for the contractile elements are predicted. This could mean that for the large distances and flight times required for migration, birds do not work any close to their fatigue limit and other factors are responsible for the swaps in such flocks. If fatigue is crucial in other situations such as complex maneuvers where more extreme torques are required it is definitely an open question.

Chapter 6

Limitation and future work

The fatigue model is a good way to predict the endurance time for high target load intensities. Indeed, in order to analyze the endurance time for small intensities, the model does not work accurately anymore. The maximal predictable endurance time is 2 hours and 39 minutes. To have such an endurance, we have to add $1.5 \cdot 10^{-7}$ to the asymptotic value. It is not possible to investigate longer endurance times. For lower intensities, the model assumes that the muscle unit does not experience the fatigue phenomenon.

As we just saw, the fatigue model is very sensitive to $T_{ce,max}$. The value of this parameter is taken theoretically because no experimental data have been collected. So in order to completely explore the fatigue model, it can be interesting to compare the theoretical values with the experimental data.

A second improvement would be to investigate the contractile element. For this thesis, I assumed that the contractile element is like a black box where we impose a length and a force and see how the elements of the model react. However, it is possible to simulate the force-length and force-velocity relationships of the contractile element. This will contribute to a more precise representation of a muscle.

In this work, I only assumed that the pectoralis muscle generates all the force during the downstroke. So I modelled only this muscle. However, the power during the upstroke is generated by the supracoracoideus muscle that works like a pulley to raise the wing. This stroke is less demanding compared to the downstroke but it can be interesting to add another muscle model that simulates the supracoracoideus muscle. This will ensure a more rigorous simulation.

Chapter 7

Conclusion

This work shows the impact of muscular fatigue in a bird's flock. It starts from an aerodynamic model of a bird flying at a constant speed and altitude. This model shows that the follower can reduce its power by being positioned behind the leader. There is an optimal position that can be obtained for which the saved power is maximal.

Then, a fatigue model is described: the so-called three-compartment muscle fatigue model. This model divides a muscle unit into 3 states: the active state, the resting state and fatigue state. This model is able to simulate the endurance time of a muscle unit. The endurance time is the time needed for a muscle to feel fatigued. We saw that this variable strongly depends on the intensity of the task. An other strong conclusion that we learned is that the endurance time does not depend on the frequency of the target load (normalized task intensity) if the fatigue and recovery rate are small enough compared to the frequency.

The third and last model that has been investigated is a muscle model. It makes the link between the aerodynamics and fatigue model. The model is composed of 2 elastic elements and one contractile element. The contractile element is assumed to be a black box. This model takes the total force applied to the system and an imposed length as input. This gives the distribution of the force and length into the different elements. In the literature, linear muscle models are presented. However, as the goal is to investigate the torque applied by a wing on the center of a bird, an angular muscle model was derived from the linear model. This angular model shows that the contractile element contracts during the downstroke which leads to a torque generation. During this stroke, the contractile element is the major component. During the upstroke, the contractile element does not contract anymore and the passive elements take the lead.

Finally, the endurance time between solo flight, leader and follower has been investigated. The endurance time is obtained from the kinematics and dynamics of a bird's wing. According to the models, a leader can fly longer before getting fatigued than a follower. This means that the fatigue phenomenon is not the leading mechanism in position swaps during collective bird migration. In an other way, for large distances and flight times required for migration, birds do not work any close to their fatigue limit. Other parameters are responsible for the swaps in such flocks.

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