# Developments of Theories of Avian Movement Strategies in Wind and Their Validation with Bio-logging Data

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Animal movement represents an interdisciplinary research field involving ecology and physics. Animal locomotion is composed of three interrelated hierarchies: micro-scale mechanisms of locomotion, often in the realm of physics; intermediate-scale regulation of speed and direction and macro-scale movement of route selection, those can significantly affect the fitness of the animal. Based on these hierarchies, animal movement strategies can be formulated as optimisation problems, yielding some theoretical predictions that can now be tested using bio-logging techniques to record animal movements. This review focuses on bird movement strategies in response to wind and aims to provide a practical overview of how theory and empirical testing with bio-logging data are carried out in the field of movement ecology.

## 1. Introduction

Animal movement is an area of research that spans two different fields: ecology and physics. The elucidation of the wide variety of movement mechanisms exhibited by animals on land, in water, and in the air is the realm of physics [1–6]. In particular, the study focusing on detailed spatio-temporal scale animal movements and the mechanical mechanisms that produce them is often referred to as biomechanics. On the other hand, real animals in the wild move over much broader scales than those studied in indoor experiments. How such movements affect the ecology and evolution of wild animals (e.g., food acquisition, survival, reproductive success, population dynamics, species distribution, etc.) is one of the central issues in ecology, and in recent years the research field dealing with this topic has been called movement ecology [7].

Biomechanics is often interested in the micro-scale mechanisms of animal movement, while movement ecology is interested in the intermediate-scale regulation of speed and direction of movement and the larger-scale movement of route selection, yet animal movement is composed of these three interrelated hierarchies (Fig. 1). First, if we focus on macro-scale movement, the route from an animal's starting point to its goal, costs such as time, energy, and risk of mortality to reach the destination will affect the fitness of the animal through its survival and reproductive success. Since the costs

associated with movement are influenced by internal factors such as morphology, cognitive ability, and experience, as well as external factors such as food distribution along the route and wind, animals are expected to select the route that lowers costs according to these factors. The travel route is the result of the integration of the travel direction and speed of the intermediate-scale animal at each time, and the energy consumption rate at each time can be formulated as a function with travel speed and direction as variables, due to the physical mechanism of movement at the micro-scale. Thus, animal route selection can be attributed to the optimization problem of finding a route that minimizes the objective function (energy consumption), and the optimal solution can be employed as testing hypotheses [8]. The approach of formulating animal behavior into optimization problems, deriving testing hypotheses, and examining them using real data has been standard in behavioral ecology [9–12], and pioneering theoretical studies on wind-dependent migration strategies of flying animals, the focus of this review, were already conducted in the late 1970s [13,14].

Until the 1970s and 1980s, the available wildlife movement data for testing these theories was mainly based on rough spatiotemporal resolution, such as visual and/or radar-based fixed-point observations and marked recapture information [15,16]. Subsequently, however, the development of behavior recorders that can be attached to birds has made it possible to record routes of wild animals over long periods starting with studies on large birds [17,18] followed by a variety of species of different sizes. Various parameters can also be measured, including acceleration [19,20], video [21–23], attitude angle [24–27], heart rate [28,29], and neural activity [30,31]. This method of acquiring behavioral data by attaching behavior loggers to wild animals is called bio-logging.

This review is targeted at physicists interested in animal movement and bio-logging data and will review the classical theories of animal movement and their validation with real data, focusing on the bird's movement strategy in response to wind. Among animal movements, there are three reasons for limiting the topic to the movement of birds in response to wind. First, bird flight is governed by physical laws that allow us to construct a model linking travel speed and energy consumption. Second, among the animal kingdom, birds are one of the most widely studied groups for bio-logging studies. Finally, wild animals encounter a variety of wind environments due to habitat differences among species and environmental changes during their travel, and thus the manipulation experiments that alter wind environments are conducted in nature, and birds' responses to wind in these different situations can be useful for inferring their migratory abilities, cognitive abilities, and movement strategies.

## 2. Optimization Problem Formulation of Bird Navigation Strategies in Response to Wind

This section outlines the interrelation among the three hierarchies that constitute animal navigation, as depicted in Figure 1. Prior to delving into the main theme, we bring forth two noteworthy aspects, namely the explication of terminologies and the flight styles of avian species.

### 2.1 Air Velocity and Ground Velocity

Here, we explicate the air and ground velocity (Figure 2). The velocity, which is defined as a vector that incorporates both speed and direction, of a bird with respect to the ground is referred to as the ground velocity. Its magnitude is termed as the ground speed, and its direction is referred to the direction of motion in this review. The velocity of the bird with respect to the air is called as the air velocity. The air velocity is the resultant vector obtained by subtracting the wind velocity from the ground velocity. The magnitude of air velocity is defined as airspeed. In the field of animal behavior, the direction of the air velocity is frequently called as the "heading direction" [32], a convention upheld in this paper. It should be noted that the heading direction may not necessarily coincide with the direction of the bird's body axis. However, the difference between the two is often assumed to be small enough to be identical [33], and thus this review will not distinguish between them in the following. A notation of the symbols in this review is listed in Table 1.

### 2.2 Flapping Flight and Soaring Flight

Avian flight can be divided into two main categories: flapping flight, in which birds move their wings to stay aloft, and gliding flight, in which they remain airborne without wing movement. Among gliding flights, soaring is a flight style that utilizes wind energy and is primarily observed in larger birds. The two major types of soaring flight are thermal soaring, which exploits updrafts [25,34–36], and dynamic soaring, which utilizes wind speed difference with altitude [33,37–42]. Although the focus of our review is on flapping flight, the theoretical framework presented here is also applicable to understanding movement strategies in soaring flight. For readers interested in learning more about movement strategies in soaring flight, we suggest consulting the references cited above as well as references [43–45].

### 2.3 Bird Movement Strategies in Response to Wind and Three Levels of Layers

The movement mechanism constitutes the first layer in the avian navigation hierarchy.

During sustained wing-flapping flight at a constant altitude, a bird's energy consumption rate (P) is inherently associated with its airspeed (V), due to the fundamental physical principles that govern avian flight.

$$P\big(V(t)\big) \tag{1}$$

V(t) is the airspeed at time t. The graph of P with V as a variable shows a U-shape (see next section).

Next, to consider the second and third layers of bird navigation hierarchy, we consider the cost of travel. The animal's position at time t, $\vec{\boldsymbol{X}}(t)$, is given by

$$\vec{\boldsymbol{X}}(t) = \int_{t_0}^{t} \Big(\vec{\boldsymbol{V}}(\tau) + \vec{\boldsymbol{W}}\big(\vec{\boldsymbol{X}}(\tau), \tau\big)\Big)\, d\tau + \vec{\boldsymbol{X}}(t_0) \tag{2}$$

where $\vec{\boldsymbol{W}}(\vec{\boldsymbol{X}}(t), t)$ is the wind velocity at time t at the bird's position $\vec{\boldsymbol{X}}(t)$. The energy consumed by the animal as it moves from time $t_0$ to t is given by

$$E(t, t_0) = \int_{t_0}^{t} P\big(V(\tau)\big)\boldsymbol{d}\tau \tag{3}$$

The energy expended by an animal per unit distance traversed" is denoted as the cost of transport (COT). This quantity is frequently employed in movement ecology to develop theoretical frameworks for animal locomotion, with COT serving as the objective function that animals are hypothesized to minimize during their travel. The COT between time $t_0$ and t is formulated as follows.

$$c(t, t_0) \equiv \frac{E(t, t_0)}{\big|\vec{\boldsymbol{X}}(t) - \vec{\boldsymbol{X}}(t_0)\big|} \tag{4}$$

By employing the COT as the currency of locomotion, predictions on animal movement can be made. It should be noted that in this review, COT is adopted as the currency of movement. Depending on the circumstances of the animals in question, alternative quantities may be more suitable as the currency. Nevertheless, even in such cases, the framework outlined in this review can be applied by replacing the objective variable.

Next, we move on to the second layer of the animal navigation hierarchy, which concerns the adjustment of airspeed and heading. Firstly, we demonstrate that the airspeed that

minimizes the COT can be deduced from the constraint P(V(t)) provided in the first layer. Let us suppose that an animal moves with a heading angle of θ during a short time interval of Δt. Under such circumstances, the COT from time t to t+Δt can be defined as follows.

$$\mathcal{C}(t) \equiv \lim_{\Delta t \to 0} c(t + \Delta t, t) \tag{5}$$

The following equation is obtained from the definition and eq (3) and (4).

$$\begin{aligned} &\mathcal{C}(t) \\ &= \lim_{\Delta t \to 0} \frac{E(t + \Delta t, t)}{\left|\vec{\boldsymbol{X}}(t + \Delta t) - \vec{\boldsymbol{X}}(t)\right|} \\ &\cong \lim_{\Delta t \to 0} \frac{P\big(V(t)\big)\Delta t}{\left|\vec{\boldsymbol{X}}(t + \Delta t)/\Delta t - \vec{\boldsymbol{X}}(t)/\Delta t\right|\Delta t} \\ &= \frac{P(V(t))}{\left|\vec{\boldsymbol{V}}(t) + \vec{\boldsymbol{W}}\big(\vec{\boldsymbol{X}}(t), t\big)\right|} \\ &= \frac{P(V(t))}{V_g(t)} \end{aligned} \tag{6}$$

Here $V_g(t)$ represents the ground speed at time t. Hence, the airspeed that minimizes $\mathcal{C}(t)$ is deduced from

$$\frac{\partial \mathcal{C}(t)}{\partial V} = \frac{\partial}{\partial V}\left(\frac{P\big(V(t)\big)}{\left|\vec{\boldsymbol{V}}(t) + \vec{\boldsymbol{W}}\big(\vec{\boldsymbol{X}}(t), t\big)\right|}\right) = 0. \tag{7}$$

The airspeed that minimize the COT is called as maximum range speed ($V_{mr}$). The $V_{mr}$ is dependent on both the heading angle and wind velocity. While we have provided the values of θ a priori, the question remains: in what direction should the bird orient its heading direction to minimize COT? In the absence of a specific goal location, as occurs when birds search for unpredictable food sources, it is advantageous to move in a direction that maximizes the distance traveled per unit of energy expended. Such a direction of movement can be derived from $\frac{\partial \mathcal{C}(t)}{\partial \theta} = 0$ and $\frac{\partial \mathcal{C}(t)}{\partial V} = 0$.

In the presence of a target location, the orientation strategy of birds is commonly classified based on three directions: the direction of travel, the direction of the wind, and the preferred direction in which the bird intends to progress. If the speed and direction of the wind remain constant, birds can minimize their energy expenditure by taking a

straight path towards the goal by offsetting the crosswind, a strategy known as complete compensation. However, if the bird's airspeed is slower than the crosswind, or if it is unable to accurately determine the direction of the distant goal, the direction of movement will deviate from the goal direction due to the crosswind, which is referred to as drift.

Some avian species exhibit migratory behavior, moving between breeding and wintering grounds during the spring and fall seasons, with some covering thousands of kilometers. On such extended spatial scales, wind patterns frequently exhibit spatial variability. In such a situation, selecting a detour route that leverages favorable tailwind assistance can result in a lower energy expenditure compared to a straight route to the destination. Suppose the bird leaves $\vec{\boldsymbol{X}}_{start}$ at time t = 0, travels along path *l*, and arrives at its goal position $\vec{\boldsymbol{X}}_{goal}$ at time t = T.

$$\vec{\boldsymbol{X}}_{goal} = \int_0^T \left(\vec{\boldsymbol{V}}(\tau) + \vec{\boldsymbol{W}}\left(\vec{\boldsymbol{X}}(\tau), \tau\right)\right) d\tau + \vec{\boldsymbol{X}}(0) \tag{8}$$

The energy expended, denoted by $E_l$, during this travel can be obtained by integrating COT along the path *l*. By converting the integrating variable to time, $E_l$ can also be expressed as the time integral of power.

$$\begin{aligned} E_l &= \int_l \mathcal{C}(t)\, ds \\ &= \int_0^T P\big(V(\tau)\big) d\tau \end{aligned} \tag{9}$$

$\int_l * ds$ denotes the integration of a variable $*$ along the curve *l*. Therefore, the optimal path selection problem can be reduced to a functional minimization problem, where we seek to find a function $\vec{\boldsymbol{V}}(t)(0 \le t \le T)$ and the travel time T that minimize the energy functional $E_l$ subject to the constraint eq (1). The optimal path can be obtained by integrating $\vec{\boldsymbol{V}}(t)$.

In this section, we have presented the relationship between the three hierarchies without delving into the specific functional forms of power and COT. Now, then, what specific predictions can be derived from the formulations and assumptions described here? In the following sections, we will give concrete form to these functions and review the movement strategies predicted from this framework and their examination

with real data.

## 3. Relationship Between Flight Speed and Power

In this section, we examine the relationship between avian flight speed and energy consumption, as well as the underlying physical mechanisms. The key takeaway is that the energy consumption rate (P) for birds flying at a constant altitude and airspeed (V) follows a U-shaped function, with V as the independent variable. This function is called the power curve.

$$P(V) = a_1 + \frac{a_2}{V} + a_3 V^3 \tag{10}$$

### 3.1 Power Curve

Here, we examine a scenario in which a bird is consistently flying at a constant airspeed V and fixed altitude by flapping its wings. It is important to note that the airflow around a bird in flight through wing flapping is highly complex and challenging to fully comprehend. Therefore, we employ a rough approximation and consider the averaged vertical and forward forces generated by the bird over a duration that is sufficiently longer than a single flap. To remain airborne, birds must maintain equilibrium between the upward force produced by wings and the gravitational force acting upon them. Furthermore, they must also balance the forward force with the drag force that acts in the direction opposite to the air velocity. Hence, the powers required for flight can be expressed as a function of airspeed (see [46] for detailed derivation). These powers are categorized as induced power, $P_{ind}$, parasite power, $P_{par}$, and profile power, $P_{pro}$.

The induced power is the power needed to generate lift that counters the gravitational force. In the case of a bird with a wingspan of b in flight, the required power $P_{ind}$, to maintain a constant airspeed of V while interacting with the air passing through a circular area with a diameter of b, and to transfer momentum to the air to offset the force of gravity, can be given by [46],

$$P_{ind} = \frac{2k(mg)^2}{\pi b^2 \rho V}. \tag{11}$$

The bird's mass is denoted by m, while b represents the wingspan, and ρ represents the density of the atmosphere. The induced power factor, k, is a constant that accounts for the deviation from a perfect circle in the region where the bird interacts with the air, and

is often taken to be 1.2 [44]. The drag force on the body is called parasite drag and is given by

$$D_{par} = \frac{1}{2}\rho S_b C_{D,par} V^2 \tag{12}$$

where $C_{D,par}$ is called parasite drag coefficient. The $S_b$ is the cross-sectional area of the body of an animal when viewed from the front called frontal body area. $P_{par}$ is product of the parasite drag and the airspeed.

$$P_{par} = \frac{1}{2}\rho S_b C_{D,par} V^3 \tag{13}$$

In addition to the induced drag that creates lift, the wing also experiences drag due to pressure and friction, which is known as profile drag. The power required to counteract this type of drag is denoted as $P_{pro}$. $P_{pro}$ has more uncertainties than $P_{ind}$ and $P_{par}$, and several different models have been proposed. The $P_{pro}$ depends on the airflow passing over the bird's wing which can be separated into two components: one due to the bird's forward motion and the other due to the flapping motion. As the former component increases in proportion to the airspeed, while the latter component decreases in proportion to airspeed as a result of decreasing flapping frequency and amplitude, [44] assumed that the profile power is constant at the typical airspeed at which birds fly. Specifically, the minimum power required for an "ideal bird" without profile power, denoted as $\min_V(P_{ind} + P_{par})$, is determined, and the profile power is then assumed to be a constant multiple of this power.

$$P_{pro} = \frac{C_{pro}}{AR}\min_V(P_{ind} + P_{par}) \tag{14}$$

AR is the aspect ratio (wingspan squared divide by wing area), and $C_{pro}$ is called the "profile power constant" and a value of 8.4 has been adopted [44]. On the other hand, [41] assumed that $P_{pro}$ depends on V [47].

$$P_{pro} = \frac{1}{2}\rho S_w C'_{D,pro} V^3 \tag{15}$$

These studies have simplified the effect of wing reciprocation on profile drag. However,

a recent study [48] has quantified the impact of wing kinematics on profile drag and developed an R package called afpt that is able to calculate a power curve based on this. The sum of the three powers, namely $P_{ind}$, $P_{par}$, and $P_{pro}$, yields the mechanical power, $P_{mec}$, required for flapping flight.

$$P_{mec} = P_{ind} + P_{par} + P_{pro} \tag{16}$$

To produce this mechanical power, the bird must activate its muscles, lungs, and circulatory system. Moreover, energy expenditure by basal metabolism also occurs. Hence, in order to determine the chemical power (*P*) required by the bird to generate $P_{mec}$, it is necessary to take into account the energy conversion efficiency of the muscles, the energy consumption of the lungs and circulatory system, as well as basal metabolism [44].

$$P = R\left(\frac{P_{mec}}{\epsilon} + M_B\right) \tag{17}$$

$M_B$ represents the organism's basal metabolic rate. The dimensionless parameter $\epsilon$, which is commonly assigned a value of 0.23 [44], denotes the efficiency of converting mechanical power into the power generated by the flight muscles. The dimensionless parameter R, which is often assigned a value of 1.1 [44], accounts for the additional power required to operate the respiratory and circulatory systems. Both $P_{mec}$ and P are dependent on the airspeed, and their respective curves are referred to as power curves (to differentiate between the two, the former is sometimes called the mechanical power curve). Although the values of parameters used in the assumed power curve and the functional form of the profile power may differ across studies, based on the previous discussion, it is expected that the power curve can be approximated using Equation (10) and has the qualitative characteristic of being U-shaped with respect to the airspeed V.

To what extent does this theoretical power curve accurately depict the actual one? Although measuring power curves poses technical challenges, [49] demonstrated that the mechanical power curves of cockatiels and ringed turtle-doves are U-shaped by quantifying the momentum these species impart on the surrounding air while flying within a wind tunnel. This was achieved by simultaneously measuring the length and force of their pectoralis muscles, in addition to the three-dimensional motion of their wings and bodies. In 2003, Particle Image Velocimetry (PIV) technology, a laser beam-

based method for quantifying airflow around a wing by tracking the motion of particles, was incorporated into animal flight research [50,51]. Subsequent studies have documented U-shaped power curves in birds, bats, and moths [52–54]. However, it is noteworthy that, although pied flycatchers exhibit a U-shaped power curve, that is flatter than the theoretical prediction as demonstrated by [53]. This is due to the parasite power changing as the bird's body pitch direction changes with airspeed. Overall, the qualitative features of the U-shaped power curve are supported by many studies, but the quantitative value may not agree with the predictions of classical theory. In subsequent sections, we will show that predictions of bird movement strategies can be classified into two types: quantitative predictions using the values of the power curve itself and qualitative predictions using the U-shaped nature of the power curve, but we note here that qualitative predictions are more robust against power curve uncertainty.

## 4. Speed Adjustment and Orientation

In this section, we investigate how avian species adjust their airspeed and heading in response to wind conditions, operating under the assumption that the cost of transport (COT) is minimized at the given moment. We commence by discussing the concept of minimum power speed and maximum range speed, employing power curves as the foundation of our analysis. Subsequently, we propose a theoretical prediction on how the maximum range speed is influenced by the wind direction in relation to the bird's travel direction, and present research studies that have empirically tested this prediction using bio-logging data. The derivation of the maximum range speed assumes that the bird is perfectly oriented in its intended travel direction. However, in reality, crosswinds can induce drift, causing the animal's trajectory to deviate from its intended path. In the latter part of this section, we will delve into the categorization of bird orientation and the underlying factors that contribute to the orientation strategy birds employ, and review empirical studies.

### 4.1 Minimum Power Speed and Maximum Range Speed

The airspeed that minimizes power during flight is referred to as the minimum power speed, whereas the airspeed that minimizes the cost of transport (COT) is known as the maximum range speed. Initially, we will explore these speeds under windless (V = Vg) conditions. For the sake of simplicity, we shall omit the notation of time of each variable. The minimum power speed is the velocity that minimizes P(V), and the maximum range speed is the speed (V) that minimizes

$$\mathcal{C} = \frac{P(V)}{V}. \tag{18}$$

As $\mathcal{C}$ is the slope of the power curve, it can be visually inferred that the point of tangency between the power curve and the origin corresponds to the maximum range speed (Fig. 3). Since the maximum range speed demands lower energy expenditure for covering the same distance compared to the minimum power speed, it is generally expected for animals to adopt the former. However, species with limited power production capabilities may opt for an airspeed closer to the minimum power speed due to the higher energy requirement per unit of time associated with maximum range speed. Shags exhibit dual locomotion capabilities, encompassing both diving and flying. However, the distinct morphological adaptations required for these two forms of locomotion give rise to trade-offs in their overall morphology. Kerguelen shags possess a specialized morphology for diving, characterized by a higher body mass, shorter wings, and smaller flight muscles. These adaptations may limit their flight performance as a consequence of such trade-offs. A study [55] revealed that the average flight time of this species is only 24 minutes per day. Furthermore, the study measured the airspeed of Kerguelen shags and compared it with the theoretical estimates of minimum power speed and maximum range speed. The findings indicated that the airspeed of this species is closer to the minimum power speed rather than the maximum range speed. Hence, it can be inferred that the morphological characteristics of this species are not conducive to generating the necessary power for achieving the maximum range speed, which enables greater distance to be covered per unit of energy consumed but requires higher energy expenditure per time as compared to the minimum power speed.

### 4.2 Maximum Range Speed in the Presence of Wind

Next, consider the maximum range speed in the presence of wind [56]. The COT is given as

$$\mathcal{C} = \frac{P(V)}{V_g} = \frac{P(V)}{|\vec{\boldsymbol{V}} + \vec{\boldsymbol{W}}|} \tag{19}$$

Let α be the angle that the air velocity makes with the ground velocity and let β be the angle that the wind velocity makes with the ground velocity (Fig. 2). Then ground speed is represented as the following.

$$V_g = W\cos\beta + \sqrt{V^2 - (W\sin\beta)^2} \tag{20}$$

V that minimizes $\mathcal{C}$ satisfies the following.

$$\frac{\partial \mathcal{C}}{\partial V} = \frac{\partial}{\partial V}\left[\frac{P(V)}{W\cos\beta + \sqrt{V^2 - (W\sin\beta)^2}}\right] = 0 \tag{21}$$

From the above equation, the following results are obtained.

$$\frac{\partial P}{\partial V} = \frac{P}{V_g\cos\alpha} \tag{22}$$

For simplicity, let us consider the situation where there is no crosswind component ($\alpha = 0$). In this case, the above equation is

$$\frac{\partial P}{\partial V} = \frac{P}{V_g}. \tag{23}$$

The airspeed that satisfies the given equation can be comprehended visually from the power curve plots. In Fig. 3, the maximum range speed is depicted for both tailwind (the orange line) and headwind conditions (the blue line). As observed from the diagram, the maximum range speed is greater for headwind and lower for tailwind compared to the no-wind condition. In the presence of a crosswind component, the airspeed is influenced by two variables: wind speed and wind direction. By taking into consideration the relationship between wind speed and maximum range speed, it can be noted that when the wind is a tailwind ($\beta = 0°$), the maximum range speed decreases proportionally with the wind speed. On the other hand, when the wind becomes a headwind ($\beta = 180°$), the relationship between wind speed and maximum range speed reverses, with higher wind speeds resulting in higher maximum range speeds, see [56] for detail.

The modulation of airspeed in response to the wind conditions by avian species has been investigated utilizing radar and bio-logging data. For instance, radar measurements of airspeed for migratory birds at 12 stations along the Northwest Passage in the Arctic region of Canada have reported a reduction in airspeed in response to the strength of the tailwind component [57]. The observation of the movement of migrating Arctic terns, employing binoculars equipped with three integrated sensors

including a laser range finder, a magnetic compass, and an elevation angle sensor, has revealed a decrease in airspeed for this species in correlation with an increase in the tailwind component [58]. Furthermore, studies have indicated that the adjustment of airspeed is also evident during foraging flights lasting several hours or minutes. Tracking with GPS has demonstrated that species such as kittiwakes and shags modulate their airspeed in accordance with the strength of the tailwind component [59,60].

It is noteworthy that we can investigate which airspeed, specifically the minimum power speed or the maximum range speed, avian species adopt by examining their adjustments in response to wind. The theoretical proposition posits that if birds adopt the maximum range speed, they would modulate their airspeed based on wind conditions. Conversely, if birds adopt the minimum power speed, their airspeed would remain unchanged regardless of wind conditions, as the minimum power speed is independent of wind. This qualitative prediction confers the advantage of being less sensitive to uncertainties in parameters and profile power of the power curve, as compared to quantitative predictions that calculate the values of the minimum power speed and maximum range speeds from a power curve. [60] reported that European shags breeding on the Isle of May in the U.K. adopt a maximum range speed, changing their airspeed according to the strength of the tailwind component This is interesting considering that Kerguelen shags, which dive and fly like European shags, adopt maximum range speed [55]. This difference may suggest that the Kerguelen shag is more focused on diving than flying. However, since [55] did not test for changes in airspeed with tailwind strength, it may be an interesting issue to test whether airspeed changes with wind for Kerguelen shags as well.

It has also been reported that animals modulate their airspeed not only in response to the tailwind component, but also to the crosswind component during migratory flights in common swifts [61] and foraging trips in bats [62]. [62] examined the correlation between wind speed and airspeed, which exhibited variation with wind direction (β) relative to the track direction, in a straw-colored fruit bat breeding in Ghana. The GPS tracking data of this species was collected at 5-minute intervals, and combined with a meteorological model that simulates local winds at a high spatio-temporal resolution (1 km x 1 km mesh, 1 min). Air velocity was calculated from the GPS-recorded ground velocity and the simulated winds to investigate how airspeed varies with wind direction and speed. The results revealed that the relationship between airspeed and wind speed changed with wind direction. In tailwind conditions ($\beta = 0$), airspeed decreased with increasing wind speed, but as the wind direction shifted from oblique back to headwind, airspeed increased with wind speed, and the rate of change of

airspeed with wind speed became more pronounced as the wind direction approached headwind conditions ($\beta = \pi$). These results indicate that this species adjusts its airspeed in response to both wind speed and wind direction, as predicted by theoretical expectations.

The adjustment of airspeed may be constrained by environmental factors and the cognitive ability of birds. [63] reported that during migration, common swifts do not adjust their airspeed at high altitudes and during nighttime. This may be attributed to the lack of visual cues available to the birds in these situations, making it difficult for them to determine their airspeed relative to the cues, leading to unsuccessful regulation of airspeed. Thus, theoretical predictions not only enable us to evaluate optimal animal behavior, but also yield valuable insights into the cognitive acumen of avian species through disparities between theoretical predictions and empirical observations.

### 4.3 Adjustment of Heading Direction

In the derivation of the maximum range speed, we have predetermined the heading angle of an organism. However, which heading direction minimizes COT? If the wind remains constant in space and time, extending from the starting point to the goal, the heading angle that aligns the travel direction with the goal direction minimizes COT [14,64]. When the travel direction aligns precisely with its intended destination to move, it is termed 'complete compensation' [32]. Nonetheless, actual avian navigation may not always exhibit this orientation. Three potential factors could contribute to this deviation. Firstly, limited airspeeds available to the bird may act as a constraint. Secondly, cognitive limitations may impair the bird's ability to perceive its position and direction accurately relative to the target. Thirdly, changes in wind patterns en route may hinder complete compensation from minimizing the energy expended to reach the goal. Hence, it is crucial to explore alternative modes of avian orientation beyond complete compensation.

When discussing the orientation of birds in response to wind, the focus often centers on the interrelationships among four directions: bird heading direction, bird travel direction, wind direction, and the Preferred Direction of Movement (PDM) [32,65,66]. PDM refers to the direction in which the bird intends to move at a specific location at time point t ($\vec{\boldsymbol{X}}(t)$)). PDM is also commonly known as the "preferred goal direction", "preferred track direction", or "intended direction of movement". It is important to note that the definition of PDM can vary depending on the study. For example, in some instances, PDM is defined as the direction of the bird's final goal point ($\vec{\boldsymbol{X}}_{goal}$) as observed from $\vec{\boldsymbol{X}}(t)$ [32,67,68], whereas in other cases where there is a clearly identifiable migratory stopover point, PDM is defined as the direction of that point as viewed from $\vec{\boldsymbol{X}}(t)$ [69].

In these cases, researchers predefine the PDM. However, in other situations, PDM is estimated from the data without making assumptions about the target point [65,70,71]. It is therefore crucial to note how PDM is defined in each study.

[32] proposed that the relationship between heading direction, travel direction, wind direction, and PDM can be classified into eight types (Fig. 4). Complete compensation is one of these types, in which the travel direction coincides with the PDM. In contrast, the state in which the heading direction coincides with the PDM, and travel direction deviates from PDM due to crosswind, is called full drift. The state between complete compensation and full drift is called partial compensation or partial drift. The state where the travel direction is more upwind than the PDM is called overcompensation. Compass downstream orientation is a compromise between speed and moving to the PDM, where the animal slightly deviates the heading direction from the wind direction to the PDM. Compass downstream orientation has the greatest deviation from the goal compared to the four strategies listed earlier, but it can achieve the highest travel speed if the airspeed is the same for all strategies. In these 5 orientation strategy has PDM, while those without PDM include passive downstream transport, downstream orientation, and upstream orientation. Passive downstream transport occurs when animals without self-propulsion flight along with wind, like wind or water, and cannot control their speed or direction. Active downstream orientation is when animals actively swim or fly in the same direction as the flow to maximize their speed and travel distance. This strategy is useful when speed and minimal energy consumption are more important than to reach a specific goal point. It allows the animal to move faster, resulting in small COT, while still moving in the preferred direction to some degree. Upstream Orientation is when animals move directly against a flow, often seen in situations to find food and mates.

### 4.4 Empirical Test of Orientation Strategies

It may not always be obvious how to identify which orientation type a species falls under from real bird movement data. This is because we do not always know the PDM of a bird. For example, when birds return to their nests after foraging, their final destination is definitely the nest, but they may take a detour to reach another stopover point along the way before reaching the goal, and such a detour in homing has been reported in the shearwaters [71,72] and Antarctic petrels [73]. [65] overcomes this difficulty and is often used as a method to quantify the degree of wind compensation and PDM of a bird from empirical data. This method allows for the estimation of bird compensation and PDM from information on the ground velocity and wind velocity (and the air velocity obtained from the difference between the two velocities) of multiple individual birds observed at a

given location. Specifically, the angle (α) between the air velocity vector and the ground velocity vector is plotted on the x-axis, and the travel direction is plotted on the y-axis, and a regression line is drawn. The slope of the regression line gives the orientation information, and the intercept gives the PDM. The orientation of the species is classified as complete compensation when (slope) = 0, full drift when (slope) = 1, partial compensation when 0 < (slope) < 1, over compensation when (slope) < 0, and compass downstream orientation when (slope) > 1. Note that this analysis assumes that the individuals used in the analysis have the same PDM. For details, please refer to the original research [65].

In the following, we review some empirical investigations that explore the influence of an animal's locomotive capabilities and cognitive faculties on its orientation in responses to wind.

First, as a study showing that the airspeed that a species can achieve has a strong influence on the orientation adopted by that species, there is an example of comparing orientation among organisms with greatly different airspeeds they can achieve [70]. This study analyzed thousands of radar tracking data from multiple spring and fall migrations of songbirds flying over southern Sweden and A. gamma moths flying over southern England in northwestern Europe and compared their orientation strategy. Both studied moths and songbirds fly at night at high altitudes (200 to 800 m for moths and 500 to 2,500 m for songbirds) and experience wind speeds of 6-22 m $s^{-1}$. Songbird airspeed is 8-16 m $s^{-1}$ while moth airspeed is slower at 3-5 m $s^{-1}$, suggesting that moths are expected to have less ability to compensate for crosswinds than birds. Indeed, moths drifted more strongly than songbirds. However, interestingly, the mean ground speed of moths was higher than that of songbirds. In other words, birds were able to reach the goal position accurately, albeit at a slower ground speed than moths due to wind compensation, whereas moths were able to reduce travel costs by actively using wind assistance, albeit at the expense of reaching the target point accurately. Thus, the study showed that each species employed an adaptive orientation strategy suited to its locomotion capabilities.

Next, we review studies exploring the cognitive abilities of birds by examining their orientation responses to wind. Discerning one's drift due to wind would conceivably be more challenging for a species in environments lacking landmarks, such as oceanic or desert regions, as opposed to terrestrial settings abundant in landmarks. Several avian species predominantly traverse land and only undertake journeys across oceans and deserts during migration. The capacity of these birds to compensate for crosswinds while navigating over the sea was investigated through the employment of radar

technology. Some studies showed that the extent of compensation of terrestrial birds decreases when navigating over the sea, in comparison to terrestrial environments. For example cranes [16] and wood pigeons [74], show comprehensive compensation on land, yet partial compensation during their flights across the sea. Compared to these species that fly over the sea for short distances and time, the ability of wind compensation is thought to have a greater impact on travel costs and mortality risk for land bird species that migrate long distances at sea during migration. Recent bio-logging technology has made it possible to record detailed bird migration routes and foraging trip tracks of seabirds, and several species have been reported to compensate wind at sea. High-resolution satellite-monitored GPS track data have demonstrated that juvenile ospreys have been shown to be capable of wind compensation over open ocean spanning distances in excess of 1,500 km [75]. By using satellite tracking, [76] documented the northward migration tracks of 25 Hudson's Hudsonian godwits over 7,000 km from Chiloé Island, Chile to the northern coast of the Gulf of Mexico, flying primarily over the sea and revealed a strong preference for complete compensation throughout the entire route of the godwits.

Wind compensation should have a significant impact on fitness not only in these birds that migrate over the sea, but also in seabirds that fly over the sea throughout their lives. During the breeding season, seabirds repeat foraging trips that travel hundreds of kilometers from their breeding grounds to feeding sites at sea, and recent studies have examined whether seabirds compensate for wind or drifted during their foraging trips [68,71,73]. Antarctic petrels, *Pagodroma nivea*, nest on the Antarctic continent, and during the breeding season they fly hundreds of kilometers over ice-covered land in strong crosswinds to forage at sea. [73] investigated whether this species exhibits wind compensation in the outward and return phases of foraging flights. The authors predicted that wind compensation would be particularly strong on the return flight, as there is no constraint to reach a specific foraging site on the outward flight, whereas there is a constraint to reach a specific destination (nest) on the return flight. In the outbound phase, this species showed partial compensation. However, contrary to expectations, the birds drifted during the return phase, and the stronger the crosswind, the more the return path deviated from the straight-line return path. In strong crosswinds (20 m/s), the return path was almost twice as long as the straight-line distance to the nest. The authors suggest that this species is able to compensate for crosswinds to some extent, and can achieve sufficient airspeed to compensate, but that drift occurs because it is difficult to assess drift on the ice-covered ground with few landmarks. [71] reported that streaked shearwaters compensate for crosswinds over the sea during their homing to their nesting islands from foraging sites

located hundreds of kilometers away. Furthermore, their PDM at sea was oriented towards the coast, deviating from their nesting island. This may indicate that they prioritise reliable arrival at their destination over energy minimisation, and actively use the coast as a landmark, because once a bird reaches the coast it can be sure to reach its nest by following the coast line. [68] analyzed the homing routes of adult female and pre-fledging juvenile frigatebirds flying over the sea, reporting that both groups compensate for wind, but adults exhibit a stronger degree of compensation. Furthermore, the extent of juvenile compensation increases with each successive trip, demonstrating the improvement of wind compensation ability through experience. Additionally, juvenile frigatebirds showed a higher degree of compensation when landmarks are visible suggesting that importance of landmarks for wind compensation in young frigatebirds.

While these studies demonstrate that seabirds exhibit wind compensation to some extent, it is interesting that these studies also reported that the degree of compensation gets stronger in environments where landmarks are likely to be available [68,71]. Furthermore, [71,73] pointed out the tendency that birds not to follow the shortest route straight back to the nest, but to take a detour by first reaching the coast or mountain range near the goal and then flying along them to return to the nest. One possible explanation for this is that the choice of a route that, although long, is certain to reach the goal by using landmarks, i.e., not only energy consumption but also the certainty of reaching the goal, may be a factor in the currency of travel (we note that this strategy of prioritizing reaching a familiar point once over the shortest route has been reported not only in flying seabirds but also in penguin homing on land [77]). Another explanation is that drifting at the beginning and compensating at the end of travel may consume less energy in response to changes in the wind environment to reach the goal (the two possibilities are not exclusive). Testing the latter possibility requires finding the optimal route in a spatiotemporally varying wind environment, which is the route selection problem that will be discussed in the next section.

## 5. Path Planning and Distribution in Response to Wind

The studies that examined orientation in the previous sections either focus only on the Heading direction at a given time or implicitly assume that the wind environment does not change significantly until the goal. However, if the wind environment changes considerably during travel, the bird needs to vary orientation over time to reduce travel costs. In this section, we examine route selection under such conditions.

### 5.1 Qualitative Prediction of Optimal Route Selection in Response to Wind

Now we will examine an example of how spatial variation in wind changes the route that

minimizes the cost of travel. We simplify the setting of eq(9) and assume that the bird's airspeed is constant, i.e., ignoring airspeed adjustment and only focus on the heading adjustment, and that the bird adopts time instead of COT as its travel cost. The route that minimizes the travel time is then given by the following equation [64,78].

$$\frac{d\theta}{dt} = -\left(\frac{du_w}{dx} - \frac{dv_w}{dy}\right)\cos\theta\sin\theta + \frac{du_w}{dy}\sin^2\theta - \frac{dv_w}{dx}\cos^2\theta \quad (24)$$

where $\theta$ is the Heading angle, which is the angle clockwise with respect to the y-axis. With the x-axis in the east and the y-axis in the north direction, consider a situation where the wind speed follows ($u_w$,$v_w$) = (-Wy,0) [m/s] between two points A,(x,y) = (0,0) [m], and B,(x,y) = (0,$10^4$) [m], 1.0 ×$10^4$m apart, i.e., the wind speed gets faster as it goes north. Fig. 5 shows the routes given by Eq. (24) for the cases of starting from point A and arriving at B and starting from B and arriving at A, when W = 8.0 × $10^{-4}$, and 1.2 × $10^{-3}$ and the bird's airspeed is 8 m/s. When there is no wind, the straight-line route is the optimal. When traveling from south to north, the optimal route is to move upwind by overcompensation in the first part of the trip, and then to partially drift in the latter part of the trip (arrows from A to B in Fig. 5). On the other hand, when moving from north to south, i.e., when the wind becomes weaker as the goal gets closer, the optimal route is to partially drift in the first part of the trip and then correct for the deviation from the goal by overcompensation in the area where the wind becomes weaker in the latter part of the trip (arrows from B to A in Fig. 5). Hence, qualitative predictions derived from theory, i.e., the strategy of "using wind assistance by drift in areas of strong winds and compensating wind in areas with weak winds".

This prediction have also been reported in actual bird migrations [69,79]. [64] found that European honey buzzards, which breed in the Netherlands in the spring and overwinter in West Africa in the winter, take detours when traveling between breeding and wintering grounds, and that these routes differ between spring and winter as a result of route selection in response to wind. The study recorded spring and autumn migrations at one-hour sampling intervals to investigate how orientations vary with geographic position during migration. During the autumn migration from the Netherlands to Africa, honey buzzards moved southeastward, overcompensating for westward winds near the Atlas Mountains in northern Africa, and then over-drifted by southwestward winds in the Sahara. In contrast, during the spring migration, honey buzzard overcompensated for the eastward winds when departing East Africa and then over-drifted with north-westward wind in the Sahel region and the north-eastward winds in the Sahara, gaining tailwind

assistance. In other words, honey buzzards are expected to select their migration route so that they can efficiently take advantage of the prevailing winds. While it has been known that some birds take detour routes and/or different routes during spring and fall migrations, [69] empirically demonstrated that the wind environment contributes to the occurrence of the detour routes.

### 5.2 Numerical Calculation of Optimal Routes in the Wind and Comparison with Real Data

So far, we have presented qualitative predictions on optimal route selection in response to wind and their examination with real data. However, it would be useful as a further analysis to calculate a route that minimizes COT based on wind information in the field in accordance with the formulation of Equation (24) and compare it with real track data. Specific methods for obtaining such routes include the Dijkstra algorithm [80] and the numerical calculation of Zermelo's solution [81]. These methods provide a route that minimizes the objective function (COT), assuming that the animal has a complete knowledge of the spatio-temporal pattern of the wind environment until the goal. It should be noted that the Dijkstra algorithm discretizes space, and therefore the travel direction should be discretized, but it has the advantage of easy implementation. On the other hand, the method of numerically computing Zermelo's solution has the advantage of allowing travel direction to be treated as a continuous variable, although the implementation of the computation is more complex than that of Dijkstra's algorithm.

[81] is, to the best of the authors' knowledge, the first study that compared the numerically computed Zermelo solution with real-wildlife tracks (In this study, the movement of animals is not to wind but to ocean currents, yet both can be treated in the same framework since both are navigation in the flow). In this study, the migration tracks of eight leatherback turtles that migrated approximately 1,000 km from their feeding sites to the East African coast, where they laid their eggs, were calculated under the current environment for the Zermelo solution and for two other migration strategies: vector orientation (a strategy that maintains a constant heading direction from departure to goal) and goal orientation (a strategy in which the heading angle is always oriented in the direction of the goal) and compared them with real tracks of turtles. The results showed that the Zermelo solution was less similar to the real routes than the other migration strategies in seven individuals, although there was variability in the routes among the individuals. In some individuals, the actual migration path was not similar to any of the three theoretically computed paths. Especially three individuals showed a characteristic pattern of large directional changes as they approached land at the end of their migration.

From these results, the authors conclude that turtles do not continually adjust their travel direction relative to the target, but only orient themselves in the approximate direction to the goal, and correction of their courses at the end of their migration is important for reaching the goal. The Zermelo solution gives the solution with the minimum travel time, i.e., the upper bound of the travel performance that the animal can achieve, assuming that the animal has a perfect knowledge of the temporally varying flow. Therefore, examining how the animal's actual path deviates from the optimal path, as shown in [81], would provide insight into the animal's movement strategy and their navigation capacity.

It would also be useful to use the Zermelo solution as a benchmark for evaluating the performance of other movement strategies [78]. By using the Zermelo solution as a benchmark, [78] investigated whether simpler movement strategies than the zermelo solution could achieve performance similar to the Zermelo solution. In [78], two systems with very different travel distances were considered: thrushes' migration over the North Sea from Norway to the Netherlands, which is about 800 km, and great snipe's nonstop intercontinental migration from Scandinavia to West Africa, which is about 6,000 km. The routes were simulated with four migration strategies: Zermelo solution, complete compensation, vector orientation, and goal orientation, and their performance (probability of reaching the goal range and travel time) of these strategies was evaluated. The results revealed that vector orientation showed almost the same performance as the Zermelo solution for systems that travel short distances, while the goal oriented strategy showed almost the same performance as the Zermelo solution for long-distance travel systems. These results indicate that simpler movement strategies than the Zermelo solution, such as goal orientation and vector orientation, can also perform similarly to the Zermelo solution, and that the performance of each strategy varies greatly depending on the distance traveled (i.e., the degree of change in wind environment). Interestingly, as a related note to the previous orientation section, complete compensation underperformed either vector orientation or goal orientation in both the thrushes and great snip systems. Complete compensation was less likely to reach the goal in the thrushes system due to strong crosswinds encountered that could not be compensated by the bird's airspeed, and in the great snip system, both the travel time was longer and probability to reach the goal were lower than that of the goal orientation strategy. This result is a good example of showing complete compensation is not always the optimal path for long-distance migration due to upper limits on bird airspeed and wind variation.

In light of the above, the Dijkstra algorithm and Zermelo's solution method may be effective in the future in terms of providing an indication of the optimal path that can

be taken by the animal. These methods assume that the bird has a complete knowledge of the spatio-temporal changes in the wind environment, but the extent to which the bird is actually aware of the surrounding wind environment is an interesting topic in its own right. In the future, it may be useful to estimate the extent to which birds are aware of the surrounding wind environment based on actual path deviations from the Zermelo solution, or to construct a more direct path planning calculation method that incorporates uncertainty in the birds' knowledge of the wind environment.

## 6 Future Issues

We have reviewed three layers of bird movement strategies in response to wind: movement mechanism, travel speed and orientation, and route selection. In this article, we focused on the optimization problem of minimizing COT, a rather classic topic in bird movement strategies. However, when examining real animal movements, deviations from the optimal solution predicted by theory are often observed. This discrepancy between theory and observations provides a starting point for new and exciting research.

For example, in this review, we assumed that COT is the currency of travel, i.e., the amount that an animal tries to minimize during its travels. In reality, however, it is possible that costs other than COT are employed or that multiple factors contribute to the currency of travel. One of these factors that has been attracting attention in recent years is the risk of extra movement costs due to fluctuations in the environment that birds cannot predict. Both the speed and the orientation adjustment and route selection that minimize the COT presented in this article assume that the animal has a perfect knowledge of the wind environment. In reality, however, the wind environment varies over a variety of spatio-temporal scales. Therefore, a movement strategy that is expected to minimize COT may require extra energy due to unexpected changes in the wind environment. In other words, movement strategies that minimize COT are not robust to fluctuations in the wind environment. The importance of the information birds have about the wind environment on their movement decisions has been recently pointed out, and recent bio-logging data allow for quantitative discussions [36,82]. In addition, the degree to which birds are aware of their environment will vary depending on the experience of each individual bird and the exchange of information in the flock[83]. In recent years, it has become possible to collect movement data from individuals of various ages, and differences in movement strategies by age have been reported for a variety of species [68,82,84,85]. In addition, some studies have also examined the flow of information within a flock [86,87].

Thus, due in part to the rapid improvement in the quality and quantity of bio-

logging data in recent years, we can expect to see further development in animal movement strategy research in the future. A key to this development, along with technology, will be the theory that provides a hypothesis to be tested. This review presented several classic testing hypotheses of bird response to wind, all of which are derived from a deterministic model. Real bird movement incorporates stochastic aspects, both in the environment encountered and in the decision-making process. We believe that the implementation of a stochastic model is useful for obtaining test hypotheses on bird decision making in stochastic environments. In the past, ideas from the field of statistical physics have often provided the springboard for new research topics in movement ecology. For example, the application of statistical physics to animal flock dynamics is a prominent research area [86–96]. As another example, the Levy Flight Hypothesis, suggesting that animals maximize their food search efficiency by adopting Levy Flights under conditions where prey density is low and prey distribution is unpredictable, has sparked considerable research and debate [97–103]. These topics are outside the scope of this paper; interested readers can find further information in the references. We hope this paper will inspire physicists interested in movement ecology, and catalyze research that integrates the theories and methodologies of physics and ecology.

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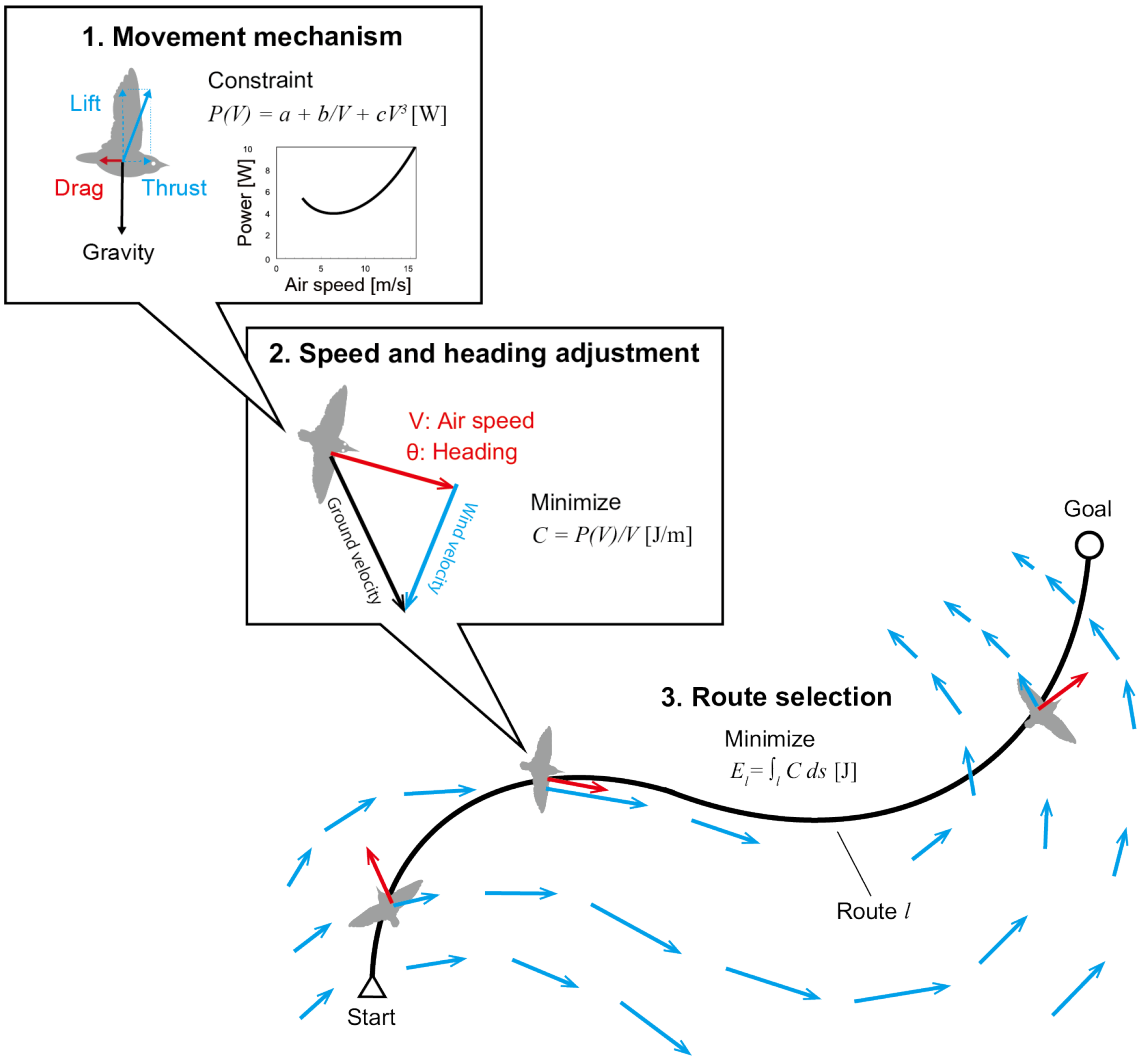


**Figure 1. (Color online) The three hierarchies constituting animal movement**

Locomotion of animals is composed of three hierarchies. The micro-scale movement mechanism, the medium-scale adjustment of speed and heading, and the macro-scale route selection.

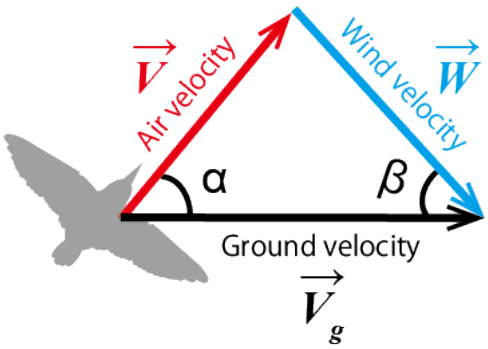


**Figure2. (Color online) Air velocity and ground velocity**

The ground velocity (black arrow) is the bird's velocity relative to the ground. The air velocity (red arrow) is the bird's velocity relative to the air. The blue arrow is the wind velocity. The ground velocity is the vector sum of the air velocity and the wind velocity.

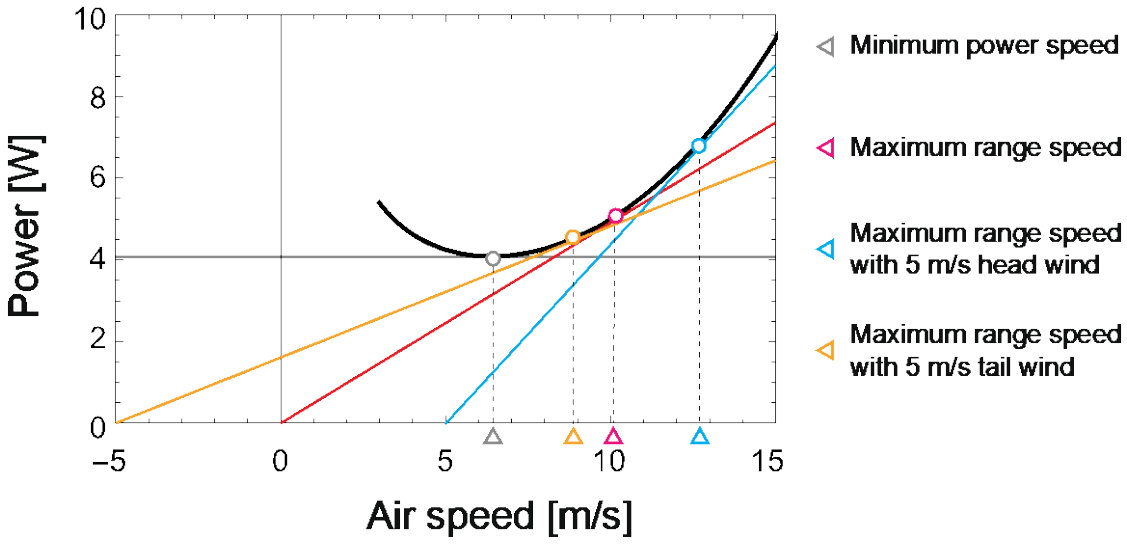


**Figure 3. (Color online) Power curve and maximum range speed**

The black line represents the power curve. The minimum power speed is the airspeed at which the power is minimized (indicated by the gray triangle). The maximum range speed in no wind conditions is given by the tangent line drawn from the origin to the power curve (red triangle). The maximum range speed with a headwind of 5 m/s is given by the tangent drawn to the power curve from air speed =5 [m/s] and power = 0 [W] (indicated by the blue triangle); the maximum range speed with a tailwind of 5 m/s is given by the tangent line drawn from air speed = -5 [m/s], power = 0 [W] to the power curve (indicated by the orange triangle).

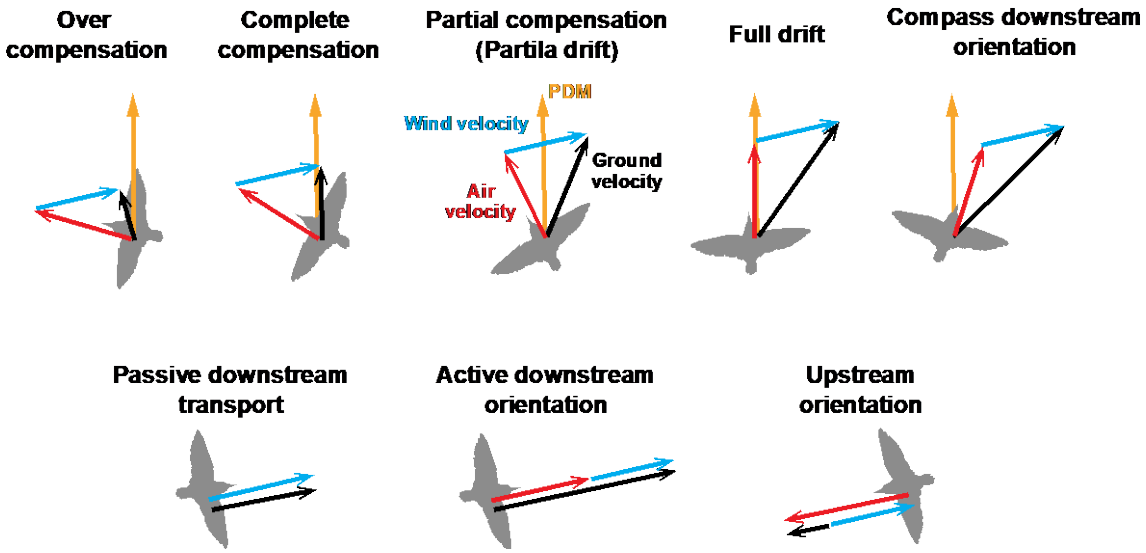


**Figure 4 (Color online) Classification of orientations in response to the wind**

Eight type of orientation of animals moving in flows proposed by Chapmann (2011)

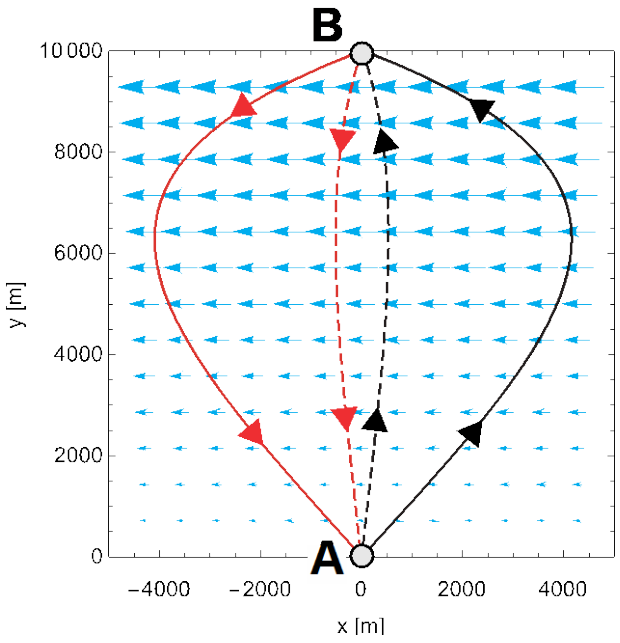


**Figure 5. (Color online) Optimal routes in spatially varying wind conditions**

Time minimizing routes under the wind field that follows $(u_w,v_w) = (-Wy,0)$ [m/s]. The blue arrows represent the wind velocities. The bird travels between two points A,(x,y) = (0,0) [m], and B,(x,y) = $(0,10^4)$ [m]. The black lines are optimal route to travel from the point A to B with $W = 1.2\times10^{-3}$ (black solid line) and $W = 8.0\times10^{-4}$ (black dashed line). The red lines are optimal route to travel from the point B to A with $W = 1.2\times10^{-3}$ (red solid line) and $W = 8.0\times10^{-4}$ (red dashed line).

| | |
|---|---|
| $\vec{\boldsymbol{V}}$ | Air velocity |
| $V$ | Airspeed ($V \equiv \lvert\vec{\boldsymbol{V}}\rvert$) |
| $\theta$ | The direction of the air velocity (Heading direction) ($\theta \equiv arg\ \vec{\boldsymbol{V}}$) |
| $\vec{\boldsymbol{V}}_g$ | Ground velocity |
| $V_g$ | Ground speed ($V_g \equiv \lvert\vec{\boldsymbol{V}}_g\rvert$) |
| $\overrightarrow{\boldsymbol{W}}$ | Wind velocity |
| $W$ | Wind speed ($W \equiv \lvert\overrightarrow{\boldsymbol{W}}\rvert$) |
| $u_w$ | x component of the wind velocity |
| $v_w$ | y component of the wind velocity |

**Table 1 Notation of symbols**