How birds weather the weather: avian migration in the mid-latitudes

Kemp, M.U.

Citation for published version (APA):

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Download date: 16 May 2020
3.1 Abstract

The impact that flows of air and water have on organisms moving through these environments has received a great deal of attention in theoretical and empirical studies. There are many behavioral strategies animals can adopt to interact with these flows, and by assuming one of these strategies a researcher can quantify the instantaneous assistance an animal derives from a particular flow. Calculating flow-assistance in this way can provide an elegant simplification of a multivariate problem to a univariate one and has many potential uses; however, the resultant flow-assistance values are inseparably linked to the specific behavioral strategy assumed. We expect that flow-assistance may differ considerably depending upon the behavioral strategy assumed and the accuracy of the assumptions associated with that strategy. Further, we expect that the magnitude of these differences may depend on the specific flow conditions. We describe equations to quantify flow-assistance of increasing complexity (i.e. more assumptions), focusing on the behavioral strategies assumed by each. We illustrate differences in suggested flow-assistance between these equations and calculate the sensitivity of each equation to uncertainty in its particular assumptions for a range of theoretical flow conditions. We then simulate trajectories that occur if an animal behaves according to the assumptions inherent in these equations. We find large differences in flow-assistance between the equations, particularly with increasing lateral flow and
increasingly supportive axial flow. We find that the behavioral strategy assumed is generally more influential on the perception of flow-assistance than a small amount of uncertainty in the specification of an animal’s speed (i.e. $< 5 \text{ ms}^{-1}$) or preferred direction of movement (i.e. $< 10^\circ$). Using simulated trajectories, we show how differences between flow-assistance equations can accumulate over time and distance. The appropriateness and potential biases of an equation to quantify flow-assistance, and the behavioral assumptions the equation implies, must be considered in the context of the system being studied, particularly when interpreting results. Thus, we offer this framework for researchers to evaluate the suitability of a particular flow-assistance equation and assess the implications of its use.

3.2 Introduction

Flows of wind and water are some of the most important environmental factors affecting the movement of volant (i.e. flying; e.g. Chapman et al., 2010; Drake and Farrow, 1988; Kunz et al., 2008; Liechti, 2006; Richardson, 1990), and natant (i.e. swimming; e.g. Cotté et al., 2007; Gaspar et al., 2006; Gibson, 2003; Luschi et al., 2003) organisms, respectively. There are several different behavioral strategies, recently reviewed by Chapman et al. (2011), that animals can adopt to make their way through these flows. By assuming a particular behavioral strategy, it is possible to simplify the potential effect of the two components of a flow (e.g. its speed and direction) into a single variable that reflects the support or resistance an animal experiences from the flow, allowing for quantitative comparisons between flow-conditions. Researchers of bird migration, for instance, frequently calculate such a variable (often termed “wind profit” or “wind effect”) to study e.g. flight altitudes (Bruderer et al., 1995b), flight speeds (Piersma and Jukema, 1990), flight range (Liechti and Bruderer, 1998), migration intensity (van Belle et al., 2007), and stopover behavior (Åkesson and Hedenström, 2000) in relation to wind conditions (see also Shamoun-Baranes et al., 2007 and references therein). Regardless of the species and the fluid through which it moves, however, correctly quantifying flow-assistance can improve our understanding of often complex biological movement processes including those involved in disease transmission (Sedda et al., 2012). Furthermore, this quantification is likely to become increasingly feasible as tracking devices become smaller (Bridge et al., 2011; Wikelski et al., 2007); animal-borne tracking systems (e.g. Wilson et al., 2008) and dedicated radar systems for animals as small as insects (Chapman et al., 2010) allow for consideration of both the relative motion and body orientation of individuals; and oceanographic (e.g. Rio and Hernandez, 2004) and atmospheric (e.g.
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Undén et al. (2002) data sets improve in resolution and accuracy.

As mentioned, the categorization and/or quantification of flow-assistance necessitate explicit and sometimes implicit assumptions of an animal’s behavior in relation to the flow. We suspect that a researcher’s perception of flow-assistance, and therefore the results of analyses using a flow-assistance variable, may be quite different depending on the behavior assumed and the flow conditions that are encountered. Further, we suspect that the resultant flow-assistance values may be sensitive to uncertainty in these assumed behaviors and that the degree of this sensitivity may also depend on the particular flow conditions. The main goals of this chapter are to provide 1) a reference for potential equations to quantify flow-assistance that explicitly describes each equation’s components and assumptions, 2) a comparison of the flow-assistance suggested by these equations for a range of flow conditions, 3) a quantification of the sensitivity of these equations to uncertainty in their respective assumptions, and 4) a methodology to simulate the trajectories that result from the behavior described by each equation. In so doing, we provide a framework for researchers to assess the appropriateness and implications of applying a particular method of flow-assistance quantification to their study system. While many examples provided throughout this chapter are related to birds, the concepts are relevant for any animal moving through air or water.

We begin with an overview of different methods and equations to quantify flow-assistance, starting with those that require the fewest assumptions and progressing through more complex techniques requiring an increasing number of assumptions. Thereafter, we quantify the difference in flow-assistance suggested by these methods and calculate the sensitivity of the associated equations to uncertainty in their respective assumptions. Finally, we model flight trajectories over a given time period using different transport models to explore the potential divergence between these methods over time and distance due to their various behavioral rules.

3.3 Flow-assistance

In this section, we discuss different methods and equations to calculate flow-assistance. Unless otherwise stated, speeds and flow-assistance values are considered in ms\(^{-1}\) and directions are considered in degrees from north (with positive angles clockwise). When we introduce a flow-assistance equation, we will give it a name (e.g. “EQ\(^{\text{Tailwind}}\)”) and use that name throughout this chapter. Table 3.1 gives the formula for each equation, and Figure 3.1 contains graphical representations of the flow-assistance values resulting from each equation for a range of theoretical flow conditions (speeds from 0-20 ms\(^{-1}\) and
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directions from 0-360°). These flow-conditions correspond to Beaufort scale 0-8 or calm through gale force wind conditions in the atmosphere. More complete assessments of these methods and equations, including formal definitions, graphical depictions, and lists of components and assumptions, are located in Appendix A.

Chapman et al. (2011) identify eight unique behavioral strategies that organisms can apply to move in a flow and give examples of animals that are thought to apply each strategy. Two of these strategies suggest that the animal travels in the direction of the flow, either actively (i.e. by applying its own forward motion in the direction of the flow) or passively. According to either of these downstream transport strategies, flow-assistance is equal to flow-speed irrespective of flow direction (EQ_{FlowSpeed}; Figure 3.1; Table 3.1). Another of these strategies suggests that the animal actively moves against the flow (i.e. upstream transport), suggesting presumably that the slower the flow the better the flow-assistance (EQ_{NegFlowSpeed}; Figure 3.1; Table 3.1).

The remaining five strategies identified by Chapman et al. (2011) assume that an animal has a preferred direction of movement (pdm) (also called a “goal direction” or “endogenous direction”) that is independent of the direction of the flow. These strategies differ primarily with respect to how deviations from the pdm are handled, and they fall into three general categories: full drift, complete compensation, and partial compensation.

3.3.1 Full drift

Following a strategy of full drift, an animal applies all of its forward motion in its pdm and makes no attempt to compensate for any lateral displacement from this pdm caused by the flow conditions. In the simplest case, flow-assistance under a full drift strategy could be defined in binary terms: the flow gives assistance in the pdm or it does not (EQ_{Binary}; Figure 3.1; Table 3.1). Because EQ_{Binary} produces a nominal, or at best ordinal, description of flow-assistance, we do not consider it in the quantitative analyses of this study. Increasing only slightly in complexity, we can define flow-assistance as the magnitude of the component of the flow along the pdm (EQ_{Tailwind}; Figure 3.1; Table 3.1), thereby ignoring any component of the flow that is perpendicular or lateral to the pdm. EQ_{Tailwind} is probably the most prolific method used to describe flow-assistance and is the de facto method being applied anytime an author refers to a tail- or headwind component (e.g. Åkesson et al., 2002; Alerstam et al., 2011; Bruderer et al., 1995; Richardson, 1978; Shamoun-Baranes et al., 2007).
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Table 3.1: Equations introduced in this chapter to quantify flow-assistance. The abbreviated name of each equation (defined in sections 3.3.3) is given in the left column, and the accompanying formula for each equation is given in the right column. In these equations, flow-assistance (\( FA \)) is determined according to the speed of the flow (\( y \)) and, depending on the equation, attributes describing an animal’s behavior or capabilities: i.e. its speed relative to the Earth (\( x \)), speed relative to the Earth in still conditions (\( x_s \)), speed relative to the flow (\( z \)), and/or proportion of compensation (\( f \)) for the component of the flow perpendicular to their preferred direction of movement. All speeds are given in the same units, typically ms\(^{-1}\). The variable \( \theta \) describes the angular difference between the direction into which the flow is moving and the animal’s preferred direction of movement. More detailed definitions of these equations are given in Appendix A.

<table>
<thead>
<tr>
<th>Name</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>EQ(^{\text{FlowSpeed}})</td>
<td>( FA = y )</td>
</tr>
<tr>
<td>EQ(^{\text{NegFlowSpeed}})</td>
<td>( FA = -1y )</td>
</tr>
</tbody>
</table>
| EQ\(^{\text{Binary}}\)        | \( FA = \begin{cases} 
0, & y \cos \theta \leq 0 \\
1, & y \cos \theta > 0 
\end{cases} \) |
| EQ\(^{\text{Tailwind}}\)        | \( FA = y \cos \theta \)                                              |
| EQ\(^{\text{Airspeed}}\)           | \( FA = y \cos \theta + \sqrt{z^2 - (y \sin \theta)^2} - z \)         |
| EQ\(^{\text{Groundspeed}}\)         | \( FA = x - \sqrt{x^2 + y^2 - 2xy \cos \theta} \)                      |
| EQ\(^{\text{C.Groundspeed}}\)       | \( FA = \begin{cases} 
x - \sqrt{x^2 + y^2 - 2xy \cos \theta}, & y \cos \theta \leq x \\
y \cos \theta - |y \sin \theta|, & y \cos \theta > x
\end{cases} \) |
| EQ\(^{\text{M.Groundspeed}}\)        | \( FA = (x_s + y \cos \theta) - \sqrt{(x_s + y \cos \theta)^2 + y^2 - 2(x_s + y \cos \theta) \cdot y \cos \theta} \) |
| EQ\(^{\text{PartialSpeed}}\)         | \( FA = y \cos \theta + \sqrt{z^2 - (f \cdot y \sin \theta)^2} - z \) |
Figure 3.1: Contour plots of flow-assistance for a range of theoretical flow conditions resulting from different behavioral strategies to move in a flow. Solid vertical lines separate the behavioral strategies (downstream transport, upstream transport, full drift, complete compensation, and partial compensation; see sections 3.3-3.3.3 for details of each) and a dashed vertical line separates equations for the same strategy with different assumptions. The abbreviated name for each equation (given in sections 3.3-3.3.3) is shown at each plot’s lower right corner. The area within each circular plot indicates particular combinations of flow direction and speed, i.e. direction in the plot indicates flow direction and the distance from the center indicates flow-speed with the edges corresponding to flow-speeds of 20 ms$^{-1}$. Continued on next page...
3.3. **FLOW-ASSISTANCE**

Figure 3.1 (continued): The contoured surface within these plots indicates the flow-assistance suggested by the equation for specific combinations of flow-speed and direction, with lighter colors indicating greater flow-assistance. A flow-assistance value of 10, for instance, indicates that, due only to the flow conditions, an animal is moved at 10 ms$^{-1}$ toward its goal, whereas a flow-assistance of -10 indicates that an animal is moved at 10 ms$^{-1}$ away from its goal. For equations in which an animal’s speed relative to the flow varies, dashed white contour lines delineate the domain of the flow conditions in which the animal’s speed relative to the flow will be between 10 and 15 ms$^{-1}$. Wherever appropriate, a preferred direction of movement (pdm) of 225° was assumed and is indicated by a large arrow in the southwest corner of each plot. If an equation required an assumed speed of any kind, it was set to 12 ms$^{-1}$. For the partial compensation equation, we show the resultant flow-assistance values produced by four different settings of the variable $f$, which describes the proportion of compensation ($f = 0$ is full drift; $f = 1$ is complete compensation).

### 3.3.2 Complete compensation

A strategy of complete compensation assumes that an animal compensates for all lateral displacement from its pdm caused by the flow conditions. To compensate for displacement, an animal must change its heading and, perhaps more importantly, its speed relative to the fixed Earth (i.e. its “groundspeed”) or its speed relative to the flow – which we will call its “airspeed” for simplicity and for comparison with literature related to flight. Note however that “swim speed”, used to describe an animal’s speed relative to the surrounding water (e.g. Castro-Santos [2005], Prange [1976], Sakai et al. [2011]), can be considered an equivalent term in this context. When quantifying flow-assistance, it is critically important to understand whether, according to a particular equation, an animal is assumed to adjust its groundspeed or airspeed.

To calculate the influence of wind on the flight time of birds, Piersma and Jukema (1990) formulated an equation that assumes an animal has a fixed airspeed and adjusts its heading (and therefore groundspeed) to maintain its pdm (EQ$^{\text{Airspeed}}$; Figure 3.1, Table 3.1). With a fixed airspeed, there are always flow conditions in which an animal cannot maintain its pdm – specifically, this occurs when the strength of the lateral component of the flow exceeds the animal’s fixed airspeed. Under these conditions, EQ$^{\text{Airspeed}}$ produces no real solution. This conforms to the definition of complete compensation given by Chapman et al. (2011), which suggests that, even if an animal intends to completely compensate, any resultant deviation from the pdm negates a strategy of complete compensation.

To explore the effects of wind on migration intensity in central Europe, Erni et al. (2002) defined a complete-compensation flow-assistance equation which assumes that, in order to maintain its pdm, an animal maintains a constant...
groundspeed by adjusting its heading and airspeed (EQ$^{\text{Groundspeed}}$; Figure 3.1; Table 3.1). As a result of these assumptions, 1) the airspeed required of the animal has no upper limit and 2) flow-assistance has a maximum value that occurs when the animal has zero airspeed (i.e. when the flow is in the pdm at the preferred groundspeed). Thus even if the flow is precisely along the animal’s pdm, flow-assistance degrades from optimum if the flow-speed is faster than the animal’s constant groundspeed.

To partly address the issue of degrading flow-assistance under potentially more supportive flow conditions, Erni et al. (2005) applied a clause to EQ$^{\text{Groundspeed}}$. The resulting equation (EQ$^{\text{C.Groundspeed}}$; Figure 3.1; Table 3.1) retains the assumption of a constant groundspeed except for conditions in which the speed of the flow along the pdm exceeds that groundspeed. Under those conditions, EQ$^{\text{C.Groundspeed}}$ defines flow-assistance as the component of the flow along the pdm minus the absolute value of any component of the flow perpendicular to the pdm; however, the animal’s reaction to these conditions (e.g. its ground- or airspeed and compensation for displacement) is ambiguous.

In this study, we introduce an additional full-compensation flow-assistance equation in which all flow conditions may be quantified, flow-assistance does not degrade from optimum under presumably more supportive flow conditions, and animal behavior is unambiguous for all flow-conditions. This new equation (EQ$^{\text{M.Groundspeed}}$; Figure 3.1; Table 3.1) is equivalent to EQ$^{\text{Groundspeed}}$ in still conditions and requires specification of the groundspeed an animal will exhibit in still conditions; however, contrary to EQ$^{\text{Groundspeed}}$, EQ$^{\text{M.Groundspeed}}$ does not assume that the animal’s groundspeed will remain the same in all flow conditions. Rather, the groundspeed the animal exhibits in still conditions is modified by adding the component of the flow along the pdm. If the strength of the component of the flow along the pdm increases (or decreases), the animal’s groundspeed increases (or decreases) equivalently. The animal then maintains that modified groundspeed by adjusting its airspeed and heading. Thus, similar to EQ$^{\text{Groundspeed}}$ and EQ$^{\text{C.Groundspeed}}$, the airspeed required of the animal according to EQ$^{\text{M.Groundspeed}}$ will fluctuate and has no upper-limit. For equations assuming variable airspeed, Figure 3.1 illustrates the domain of flow-conditions in which an animal’s airspeed is between 10 and 15 ms$^{-1}$, which is reasonable for a passerine (Bloch and Bruderer, 1982; Bruderer and Boldt, 2001).

### 3.3.3 Partial compensation

The methods introduced so far assume that animals either completely compensate for displacement from their pdm or are fully drifted by any lateral component of the flow. The myriad of potential strategies between these ex-
tremes, generally referred to as strategies of “partial compensation” or “partial drift”, describe a situation in which an animal is drifted somewhat away from its pdm but not as far away as it would be drifted under a full drift strategy. To reduce lateral displacement from its pdm caused by the flow conditions, an animal may alter its heading or airspeed – adjusting either of which independently resulting in a concomitant change in the animal’s groundspeed – or a combination of the two.

One method to quantify flow assistance for a partial compensation strategy is to assume that an animal has a fixed airspeed and compensates for a specified proportion of the lateral component of the flow (EQ\textsuperscript{PartialSpeed}; [Figure 3.1, Table 3.1]) by adjusting its heading and therefore groundspeed. EQ\textsuperscript{PartialSpeed} contains a parameter \((f)\) describing the proportion of the lateral component of the flow for which the animal will compensate. Of particular appeal is that this equation can encompass not only strategies of partial compensation but also strategies of full drift and complete compensation depending on the value of \(f\) – setting \(f\) to zero reduces EQ\textsuperscript{PartialSpeed} to EQ\textsuperscript{Tailwind} (i.e. the animal is fully drifted), while setting \(f\) to one reduces EQ\textsuperscript{PartialSpeed} to EQ\textsuperscript{Airspeed} (i.e. the animal completely compensates). As with EQ\textsuperscript{Airspeed}, EQ\textsuperscript{PartialSpeed} can also produce no real solution in some flow conditions. This occurs when, given its fixed airspeed, an animal cannot compensate for the specified proportion of the lateral component of the flow.

### 3.3.4 Other strategies

Thus far, we have discussed six of the eight behavioral strategies outlined by [Chapman et al. (2011)](Chapman et al. 2011), but we have neglected mention of “compass-biased downstream orientation” and “over-compensation”. In the context of quantifying flow-assistance, compass-biased downstream orientation is indistinguishable from a strategy of partial compensation and could therefore be represented by an equation such as EQ\textsuperscript{PartialSpeed}. Over-compensation, however, describes a situation in which an animal has a (local or immediate) pdm that clearly differs from the pdm assumed by the researcher. Thus in the context of quantifying flow-assistance, the concept of over-compensation is not so much a unique behavioral strategy as an alternative specification of the pdm.

### 3.4 Methods

#### 3.4.1 Sensitivity analysis

Considering the different behavioral assumptions inherent in these flow-assistance equations, we performed sensitivity analyses to determine whether (and to
what degree) perceived flow-assistance depended upon 1) the equation applied and 2) uncertainty in each equation’s assumptions.

We first calculated the absolute difference in flow-assistance between the equations for a range of theoretical flow conditions (speeds from 0-20 ms$^{-1}$ and directions from 0-360°) and show the results graphically. Further, we calculated the average of the flow-assistance values suggested by each equation over the same range of theoretical flow conditions to serve as a measure of the relative “optimism” of the flow-assistance equation – more optimistic equations therefore suggest larger estimates of flow-assistance on average than less optimistic equations. We assumed a speed (ground- or air- depending on the equation) of 12 ms$^{-1}$, which is representative of the airscrews calculated for many migrating passerine species (Bloch and Bruderer, 1982; Bruderer and Boldt, 2001), and a pdm of 225°. When considering EQ$^{\text{PartialSpeed}}$, we set $f$ (i.e. the proportion of compensation) to 0.5.

We then determined the sensitivity of each equation to uncertainty in its particular assumptions for a range of theoretical flow conditions (speeds from 0-20 ms$^{-1}$ and directions from 0-360°) and show these differences graphically. For each equation that assumes a pdm, we calculated the difference in flow-assistance that resulted from a change in the pdm of 1°, 10°, and 30° (i.e. by comparing a pdm of 225° with pdms of 226°, 235°, and 255°). For each equation that assumes a ground- or airspeed, we calculated the difference in flow-assistance that resulted from a change in the assumed speed of 1, 2, and 5 ms$^{-1}$ (i.e. by comparing a speed of 10 ms$^{-1}$ with speeds of 11, 12, and 15 ms$^{-1}$). For EQ$^{\text{PartialSpeed}}$, we calculated the difference in flow-assistance that resulted from a change in $f$ of 0.1, 0.25, and 0.5 (i.e. by comparing $f$ set to 0.1 with $f$ set to 0.2, 0.35, and 0.6). When not being tested, we set the pdm to 225°, any speed-related assumption to 12 ms$^{-1}$, and $f$ to 0.5. We also performed an analytical assessment of the sensitivity of each equation to uncertainty in its various assumptions by calculating the partial derivative of the equation with respect to each assumption. These analytical results can be found in Appendix A.

### 3.4.2 Simulating trajectories

We expected that the suitability of a particular flow-assistance equation would depend upon not only the assumptions applied, but also on the study system including the actual conditions encountered. Further, we expected that the consequences of applying a particular equation may accumulate over time and distance. Thus, we developed a dynamic model for movement of individuals in a fluid medium, incorporating the concepts of a pdm and constraints on air- and groundspeed as specified by the flow-assistance equations. This “FLow-
Assistance Trajectory model” (hereafter FLAT model) is described in detail in Appendix B and has been implemented in the open-source R language (R Development Core Team, 2010). The FLAT model can simulate the trajectory that an animal would exhibit in the real world if it acted according to the behavioral rules of a particular equation.

The FLAT model is an extension of the RNCEP package described in Chapter 2. The trajectory simulator function developed for this study, NCEP.flight(), makes use of the NCEP.interp() function to interpolate atmospheric data from the National Centers for Environmental Prediction (NCEP)/Department of Energy (DOE) Reanalysis II dataset (Kanamitsu et al., 2002) to any time and location.

We simulated the flight of a nocturnal passerine departing at sunset from the southern tip of Norway (58°N 7°E) intent on arriving at a particular goal location (54°N 0.161°W) on the coast of the U.K. For every night in October from 1980-2010, we simulated a trajectory if the equation being tested suggested positive flow-assistance at the time of take-off. We assumed that this simulated bird was able to fly for 13 hours with a pdm of 225°. We assumed a speed (ground- or air- depending on the equation) of 12 ms⁻¹, and we used wind conditions at the 925 mb pressure level. We considered whether or not a bird arrived within 50 km of its goal location (i.e. 54°N 0.161°W) as a primary measure of its success. We considered whether or not the bird arrived at the coast of the U.K. as a secondary measure of its success. We ended a night’s simulation as soon as the primary measure of success was achieved but otherwise allowed the simulation to run the full 13 hours. If at some point during a simulation the bird could not perform the actions specified by the flow-assistance equation (e.g. with EQ\textsuperscript{Airspeed} the bird could not fully compensate with its fixed airspeed), the simulation for that night ended and the bird made no further progress. Otherwise, we placed no restrictions on the bird (e.g. with EQ\textsuperscript{Groundspeed} we did not place an upper limit the bird’s airspeed); however, for equations that assumed variable airspeed (i.e. EQ\textsuperscript{Groundspeed} and EQ\textsuperscript{M.Groundspeed}), we also reported measures of performance that resulted if we ended the simulations when the airspeed required of the bird was outside an acceptable range, which we defined as being between 10 and 15 ms⁻¹. We recorded the bird’s location and its (ground- and air-) speed as well as the flow conditions after each hour of the simulation.

Note that EQ\textsuperscript{C.Groundspeed} does not specify the behavior of the animal for all flow conditions, so we did not consider that equation in these simulations. Further, EQ\textsuperscript{NegFlowSpeed} does not produce positive flow-assistance values, so we initiated take-off for that equation only on nights when flow-speed was less than the bird’s assumed airspeed (i.e. 12 ms⁻¹).
From these simulated trajectories, we considered differences between the flow-assistance equations with regards to 1) the proportion of nights that take-off was initiated 2) the average distance to the goal at the end of the simulation, 3) the proportion of nights with a successful arrival according to our primary criteria (i.e. arrival within 50 km of the goal location), and 4) the proportion of nights with successful arrival according to our secondary criteria (i.e. arrival at the U.K. coast). We also visualized the resultant trajectories on a map.

3.5 Results

3.5.1 Sensitivity analysis

The difference in flow-assistance between each equation for a range of theoretical flow conditions is visualized in Figure 3.2. In general, these equations differ most with increasingly supportive axial flow and increasing lateral flow. The equations agree most often with prohibitive axial flow, and most equations agree completely with prohibitive flows containing no lateral component. Figure 3.2 also indicates the average flow-assistance resulting from each equation for the range of flow conditions we tested. These averages suggest that the less compensation assumed by an equation the more optimistic are its estimates of flow-assistance. We note, however, that these averages (particularly those of $\text{EQ}_{\text{PartialSpeed}}$, $\text{EQ}_{\text{Airspeed}}$, $\text{EQ}_{\text{M.Groundspeed}}$, $\text{EQ}_{\text{Groundspeed}}$, and $\text{EQ}_{\text{C.Groundspeed}}$) are dependent on the ground- or airspeed assumed and the range of flow-speeds that are considered.

The sensitivity of each individual equation to uncertainty in its particular assumptions is visualized in Figure 3.3. Clearly, larger errors in any given assumption produce larger differences in suggested flow-assistance. Interestingly, shifting the pdm produces a line of zero difference for flows along the axis between the two directions; however, differences tend to increase with increasing lateral flow and increasingly supportive axial flow that is not along this line of zero difference. For the ranges of uncertainty we tested, equations were more sensitive to the pdm than to airspeed, groundspeed, or $f$. Nevertheless, differences in flow-assistance from minor uncertainty in a particular assumption (i.e. $< 10^\circ$ for the pdm, $< 5$ ms$^{-1}$ for the ground- or airspeed) are generally smaller than differences in flow-assistance between the equations themselves (cf. Figure 3.3). For any given flow conditions, the partial derivative equations in Appendix A allow for the explicit calculation of the sensitivity of a particular equation to a particular assumption.
Figure 3.2: This figure contains 1) a main table with contour plots indicating the absolute difference in flow-assistance between different flow-assistance equations for a range of theoretical flow conditions and 2) a sub-table with the average flow-assistance suggested by each equation in ms$^{-1}$. In both tables, the equations are listed from top to bottom by decreasing average flow-assistance for the range of flow conditions we tested. Continued on next page...
Figure 3.2 (continued): In the main table, the contoured surface within the plots indicates the absolute difference (ms\(^{-1}\)) in flow-assistance between the equation in the row name and the equation in the column name, with darker shades of gray indicating greater difference; a key is given at the bottom of the figure illustrating the ranges encompassed by each shade of gray. Areas of the contoured surface in white have no real solution. Location within each circular plot indicates a particular combination of flow direction and speed, i.e. direction in each plot indicates flow direction and the distance from the center indicates flow-speed with the edges corresponding to flow-speeds of 20 ms\(^{-1}\). Wherever appropriate, a preferred direction of movement (pdm) of 225° was assumed and is indicated by the large arrow in the southwest corner of each plot. If an equation required an assumed speed of any kind, it was set to 12 ms\(^{-1}\). For EQ\(^{\text{PartialSpeed}}\), we set \(f\), i.e. the proportion of compensation, to 0.5.

3.5.2 Simulating trajectories

The trajectories that resulted from our simulation are shown graphically in Figure 3.4 and summary information for these trajectories is given in Table 3.2. Generally speaking, more optimistic equations (i.e. equations assuming less compensation and producing higher estimates of flow-assistance) are associated with a higher percentage of nights with take-off; however, these equations also resulted in larger distances to the goal location at the end of the simulation and a lower chance of successful arrival. We note that, had we run the simulation for 14 rather than 13 hours, EQ\(^{\text{Groundspeed}}\) would have a 100% success rate for both the primary and secondary measures. Furthermore, recall that we allowed negative flow-assistance values at take-off for EQ\(^{\text{NegFlowSpeed}}\). Had we not, the number of nights with take-off for that equation would have been zero. Based on the current simulation parameters and wind conditions, EQ\(^{\text{M.Groundspeed}}\) resulted in the highest proportion of successful arrivals and the highest absolute number of successful arrivals according to either of our measures of success; however, when restrictions were placed on airspeed, the performance of equations assuming variable airspeed (i.e. EQ\(^{\text{Groundspeed}}\) and EQ\(^{\text{M.Groundspeed}}\)) worsened considerably.

3.6 Discussion

Calculating flow-assistance is a useful way to evaluate the complex and non-linear effects of the two components of a flow (e.g. its speed and direction) on aspects of animal movement in static or dynamic models. In particular, calculating flow-assistance facilitates quantitative comparisons between different flow-conditions. We have shown that different definitions of flow-assistance are linked to different behavioral rules and, depending on the behavioral rules as-
Figure 3.3: Contour plots indicating the absolute difference in flow-assistance, for a range of flow conditions, produced by uncertainty in an equation’s assumptions. Continued on next page...
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Figure 3.3 (continued): The assumption being tested is indicated in the major column header (cells shaded black), and the equation for which that assumption is being tested is indicated in the minor column header (cells shaded white). Within each group, equations are presented from left to right by decreasing average flow-assistance for the range of flow conditions we tested (see Figure 3.2). Row names indicate the amount of difference (i.e. uncertainty) in a given assumption. The contoured surface within these plots indicates the absolute difference in flow-assistance produced by the specified change in the specified assumption, with darker colors indicating greater difference; a key is given at the bottom of the figure illustrating the ranges encompassed by each shade of gray. Areas of the contoured surface in white have no real solution. Location within each circular plot indicates a particular combination of flow direction and speed, i.e. direction in the plot indicates flow direction and the distance from the center indicates flow-speed with the edges corresponding to flow-speeds of 20 ms$^{-1}$. When not being tested, the preferred direction of movement (pdm) was set to 225° (indicated by a large arrow in the southwest corner of each plot), any assumed speed was set to 12 ms$^{-1}$, and $f$ (i.e. the proportion of compensation in EQ$^{\text{PartialSpeed}}$) was set to 0.5. When testing the effects of uncertainty in the pdm, the alternative pdm is indicated by a smaller arrow in the west-southwest of the plot.

...assumed, the perception of flow-assistance can be quite different for the same flow conditions. These differences can shape our impression of the efficiency and/or success of an animal’s movement through a flow. Ultimately, whether or not particular flow conditions are considered supportive at all is dependent on the equation applied. Thus, results derived through the use of a flow-assistance equation must be interpreted in the context of the behavior assumed by that equation, and we expand upon this point in sections 3.6.1–3.6.4.

3.6.1 Compensation and flow-assistance

The flow-assistance equations presented in this study describe varying degrees of compensation for lateral displacement, which can affect the flow-assistance an animal experiences for given flow conditions. Extreme examples of compensation for lateral displacement are represented by EQ$^{\text{FlowSpeed}}$ and EQ$^{\text{NegFlowSpeed}}$: the former describing a strategy of “ultimate drift” and producing the largest (i.e. most optimistic) estimates of flow-assistance and the latter a strategy of “ultimate compensation” and the smallest (i.e. most pessimistic) estimates of flow-assistance. What is highlighted by these extremes is that for any given flow conditions, more compensation results in lower flow-assistance values. In other words, an equation that assumes more compensation will never produce a larger estimate of flow-assistance than an equation that assumes less compensation, since compensation reduces flow-
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assistance while drifting away from the pdm does not. Thus, the amount of compensation specified by an equation implicitly defines, for the system being studied, the importance of lateral displacement from the pdm; EQ\textsuperscript{Tailwind}, which assumes no compensation for displacement from the pdm, implies that drifting away from the pdm is of no consequence, while the complete compensation strategy underlying EQ\textsuperscript{Airspeed} implies that it is necessary that the animal maintains its pdm.

It is possible that an animal switch between compensation strategies. For instance, an animal could completely compensate when the lateral flow component is small and begin to partially compensate or even fully drift as the lateral flow component increases. Alternatively, an animal could exhibit a full drift strategy up to some threshold of lateral displacement and only begin to (partially) compensate thereafter [McLaren et al. 2012]. Klaassen et al. (2011) suggest that the degree of compensation by migrating raptors can vary dramatically by geographical region and also in relation to the flow conditions encountered. Thus for a given species, displacement from the pdm may be more or less important in different locations, and displacement to one side of the pdm may be more or less important than displacement to the other side. Conversely, Horton et al. (2011) observed migrating humpback whales completely compensating for displacement from their pdm through variable ocean currents for distances of 200 km or more.
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Table 3.2: A summary of the trajectories simulated for each flow-assistance equation is given. Included are the percentage of nights during October 1980-2010 that take-off was initiated (i.e. flow-assistance was positive, except considering EQ_{NegFlowSpeed}, see section 3.4.2), the average distance (km) to the goal location (54°N 0.161°W) at the end of the simulations, the percentage of nights with take-off that resulted in a successful arrival according to our primary criteria (i.e. < 50 km from the goal location), and the proportion of nights with take-off that resulted in a successful arrival according to our secondary criteria (arrival at the U.K. coast). Values in parentheses indicate, for equations assuming variable airspeed, results that occurred when airspeeds were restricted to between 10 and 15 ms\(^{-1}\). The equations are listed from top to bottom by decreasing optimism (i.e. decreasing average flow-assistance for the range of flow conditions we tested).

<table>
<thead>
<tr>
<th>Equation</th>
<th>Nights with take-off (% of 961)</th>
<th>Average distance to goal (km)</th>
<th>Primary successful arrival (%)</th>
<th>Secondary successful arrival(%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>EQ_{FlowSpeed}</td>
<td>100</td>
<td>1296</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>EQ_{Tailwind}</td>
<td>29</td>
<td>364</td>
<td>8</td>
<td>51</td>
</tr>
<tr>
<td>EQ_{PartialSpeed}</td>
<td>26</td>
<td>207</td>
<td>17</td>
<td>60</td>
</tr>
<tr>
<td>EQ_{Airspeed}</td>
<td>18</td>
<td>100</td>
<td>63</td>
<td>63</td>
</tr>
<tr>
<td>EQ_{M.Groundspeed}</td>
<td>20 (17)</td>
<td>67 (132)</td>
<td>82 (61)</td>
<td>82 (61)</td>
</tr>
<tr>
<td>EQ_{Groundspeed}</td>
<td>18 (8)</td>
<td>68 (316)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>EQ_{NegFlowSpeed}</td>
<td>66</td>
<td>623</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

3.6.2 The preferred direction of movement

A fundamental assumption of most of the equations in this chapter is that an animal has a pdm that is known. In fact, the pdm can be the most difficult variable to ascertain in these equations. While the dynamics of a flow and the groundspeed of an individual animal can be measured directly, and the airspeed of the animal then derived, it can be difficult to measure the pdm of a free-moving animal, particularly at smaller scales. There are some instances when researchers can presume a pdm with a high degree of certainty, for instance when flow-speeds are negligible or when an animal is nearby and returning to a known location such as its nest. Often, however, the pdm must be estimated from observed behavior, for example using orien-
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tation cages (Åkesson and Sandberg, 1994; Emlen and Emlen, 1966) or radar (Chapman et al., 2010; Liechti et al., 2012). Regardless, this estimation can be problematic. Nievergelt et al. (1999) suggest that differences in pdm can occur between caged and free-moving animals, and Green and Alerstam (2002) show how non-random distributions of flow conditions may bias estimations of drift (and implicitly estimations of the pdm) in migrating birds. Importantly, we have found that small errors in the pdm (i.e. < 10°) are generally less influential on the perception of flow-assistance than the overall behavioral strategy assumed.

While we retained a static pdm in our trajectory simulation, it is perfectly legitimate to assume that an animal adjusts its pdm at different spatial and temporal scales. For instance, hatchling loggerhead (Caretta caretta) and green turtles (Chelonia mydas) orient offshore, often against approaching waves (Lohmann and Lohmann, 1992; Salmon and Lohmann, 1989), in an initial “frenzied” swim to reach deeper water where they then make use of favorable ocean currents for dispersal (Hays et al., 2010; Salmon and Wyneken, 1987). Avian research also suggests that the pdm may not be consistent along the entire migratory journey (Fortin et al., 1999; Liechti et al., 2012; Thorup and Rabøl, 2001), and local adjustments to the pdm are especially likely in species avoiding a barrier or obstacle (e.g. Alerstam, 2001) or making use of thermal and/or orographic uplift (Brandes and Ombalski, 2004; Leshem and YomTov, 1996). To address this variability, Mandel et al. (2008) explored an elegant method of determining the pdm at local scales through the use of an autoregressive moving average of previous movement.

Depending on the level of knowledge an animal has of its own location in relation to the location of its end goal, the animal could alter its pdm at intervals along its journey to compensate for previous displacement (see e.g. Richardson, 1990b). In so doing, the animal could apply a full drift or partial compensation behavioral strategy and still arrive at a very specific goal location, and Alerstam (1979) explored the optimality of such behavior for different flow conditions. The FLAT model presented in this study can simulate this type of behavior allowing a researcher to consider flow-assistance according to a dynamic pdm that automatically adjusts toward a specified goal location.

3.6.3 Ground- and airspeed

Many of the equations discussed in this chapter require an assumed travel speed, given as either a ground- or airspeed. While we have shown that a small degree of uncertainty in these assumed speeds is less influential on the perception of flow-assistance than the equation applied, it is important for
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For instance, with $\text{EQ}^{\text{Groundspeed}}$ an animal’s groundspeed is presumed constant and, to completely compensate for drift, heading and airspeed are altered and are not constrained. The trajectories produced by $\text{EQ}^{\text{Groundspeed}}$ in our simulations exhibit airspeeds ranging from 0.6 to 28.2 ms$^{-1}$ (Figure 3.4), which exceed both the upper and lower range of realistic and observed airspeeds for passerines (Bruderer and Boldt [2001], Pennycuick [2008]). Thus, the assumptions underlying $\text{EQ}^{\text{Groundspeed}}$ – as well as those underlying $\text{EQ}^{\text{M.Groundspeed}}$ – may be inappropriate to apply in a simulation because of the potentially unrealistic airspeeds required to maintain full compensation. As we have seen, restricting the airspeeds allowed by these equations can considerably influence the results of analyses (see Table 3.2). $\text{EQ}^{\text{Groundspeed}}$ is a legitimate measure of flow-assistance, however, since any airspeed required of the animal decreases flow-assistance, and unrealistic airspeeds inevitably lead to poor flow-assistance values. Furthermore, $\text{EQ}^{\text{Groundspeed}}$ may be of particular use in some instances as it is the only equation we discussed that can reflect a situation in which an animal is assumed to dislike flows above a certain speed, even in a desirable direction.

3.6.4 Range estimation

Some of these equations have been used in an effort to incorporate flow effects into models to estimate the distance an animal can travel with a given amount of energy (Alerstam and Lindström [1990]). In a simple case, Weber et al. (1998) and Weber and Hedenström (2000), using $\text{EQ}^{\text{Binary}}$, expanded their modeled bird’s flight range by 20% under supportive conditions (i.e. “good” winds) but left it unchanged under prohibitive conditions (i.e. “bad” winds). Others have used the quantitative measure of flow-assistance from $\text{EQ}^{\text{Tailwind}}$ (e.g. Delingat et al. [2008], Liechti and Bruderer [1998]) to modify flight range.

When incorporating flow-assistance into models to estimate swim or flight range, that range will be larger with flow-assistance equations that allow drift from the pdm than with equations that do not. Therefore when applying an equation that implicitly allows or ignores drift (e.g. $\text{EQ}^{\text{PartialSpeed}}$ or $\text{EQ}^{\text{Tailwind}}$), a researcher must be comfortable making one of the following two assumptions: 1) the animals under consideration will be drifted by whatever lateral flow is present (or remaining after partial compensation), but the displacement due to this drift is unimportant, or 2) the animal will compensate for whatever lateral flow is present (or remaining), but the energy required to do so is unimportant. Delingat et al. [2008], for instance, presumed the latter, stating that the birds in their study were not engaged in a full drift
strategy but rather that “the effects due to wind drift compensation... will be small in comparison with the overall range estimates.” Alternatively, the first assumption may be satisfied if, for the area or trajectory being studied, lateral flows are minimal enough or equally distributed across both sides of the pdm such that the resulting drift does not force the animal outside the bounds of its geographical goal. Our trajectory simulation showed that by allowing drift an animal may be unable to arrive at a specific goal location. Consider that only 8% of the trajectories simulated according to \( EQ^{\text{Tailwind}} \) resulted in a successful arrival according to our primary criteria (i.e. within 50 km of the goal location; Figure 3.4 and Table 3.2). However, this rate of success increases dramatically to 51% if the bird needs only to reach the U.K. mainland (Figure 3.4 and Table 3.2). Therefore, a flow-assistance equation that allows drift may overinflate estimates of an animal’s potential range if the system in question requires the animal to arrive at a very specific location and does not allow the animal to adjust its pdm during the journey. The FLAT model can be used to examine this possibility explicitly and determine if, for a particular system and behavior, an animal would be drifted outside the bounds of its goal location.

### 3.7 Conclusion

While a great deal of the literature cited and analyses performed in this chapter are avian-related, the concepts generally apply to all organisms traveling through a fluid environment. \( EQ^{\text{FlowSpeed}} \) can even be applied when considering objects such as seeds and pollen that have no means of self-propulsion or drift passively with the flow (Nathan et al., 2005). Nonetheless, the particulars of each system deserve consideration as there remain important differences relevant to the quantification of flow-assistance between animals and their mediums of travel: e.g. in contrast to a flying animal, a swimming animal may not need to maintain a minimum speed relative to the flow in order to stay afloat.

Quantifying flow-assistance according to a particular method implies certain behavioral rules. These behavioral rules, which govern an animal’s reaction to a flow or determine the relative importance of the flow, reflect an animal’s desired goals. These goals may be evaluated in intervals from seconds to seasons, or even lifetimes and likely fluctuate depending on factors such as life history stage (e.g. Luschi et al., 2003, Thorup et al., 2003), available energy (e.g. Schmaljohann and Naef-Daenzer, 2011, and references therein), time of the season (Ellegren, 1993, James et al., 2005, Karlsson et al., 2012), distance to their desired goal (Karlsson et al., 2012, Liechti, 1995), and the
specific flow conditions in an area (Brodersen et al., 2008; Gaspar et al., 2006; Weber et al., 1998). A flow-assistance equation should therefore stipulate behavioral rules that reflect these goals, and the results of analyses must then be interpreted within the context of that behavior. Alternatively when the goals of an animal are uncertain, determining which flow-assistance equation best reproduces observed actions can be informative of an animal’s behavior and desires. EQ\textsuperscript{PartialSpeed} may be particularly attractive in this context as it can be varied by tuning one parameter controlling the degree of compensation.

In this chapter, we have outlined a framework to assess the appropriateness and implications of applying various methods to quantify flow-assistance. As demonstrated in this study, flow-assistance equations (and implicitly their assumptions) can be incorporated in a dynamic simulation model to study the specific implications of assuming a particular behavioral strategy, which can be quite informative when exploring the potential integration of flow-assistance in movement research.

Acknowledgments

We would like to thank Hans van Gasteren for discussion and comments on an earlier version of this manuscript and the IBED writers’ club for their valuable critiques and suggestions. NCEP Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/. Our migration studies are facilitated by the NLeSC (http://www.esciencecenter.com/) and BiG Grid (http://www.biggrid.nl) infrastructures for e-Science.