



Quantifying flow-assistance and implications for movement research

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HIGHLIGHTS

- ▶ Methods to quantify flow-assistance for flying and swimming animals are examined.
- ▶ We examine each method's assumed behaviors and their sensitivities to uncertainty.
- ▶ Perceived flow-assistance differs more between methods than from minor uncertainty.
- ▶ We provide software to simulate trajectories using publicly available wind data.
- ▶ Simulated bird flights show contrasting results due to different assumed behaviors.

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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 that 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 on 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. $\leq 5 \text{ ms}^{-1}$) or preferred direction of movement (i.e. $\leq 10^\circ$). Using simulated trajectories, we show that 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.

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1. 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

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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., 1995), 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. 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 paper 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 manuscript 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.

2. 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^{Tailwind}”) and use that name throughout this paper. Table 1 gives the formula for each equation, and Fig. 1 contains graphical representations of the flow-assistance values resulting from each equation for a range of theoretical flow conditions (speeds from 0 to 20 ms^{-1} and directions from 0° to 360°). These flow-conditions correspond to a 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}; Fig. 1; Table 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}; Fig. 1; Table 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.

2.1. 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

Table 1

Equations introduced in this paper to quantify flow-assistance. The abbreviated name of each equation (defined in Sections 2–2.3) 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 θ 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.

Name	Formula
EQ ^{FlowSpeed}	$FA = y$
EQ ^{NegFlowSpeed}	$FA = -1 * y$
EQ ^{Binary}	$FA = \begin{cases} 0, & y \cos \theta \leq 0 \\ 1, & y \cos \theta > 0 \end{cases}$
EQ ^{Tailwind}	$FA = y \cos \theta$
EQ ^{AirSpeed}	$FA = y \cos \theta + \sqrt{z^2 - (y \sin \theta)^2} - z$
EQ ^{Groundspeed}	$FA = x - \sqrt{x^2 + y^2 - 2xy \cos \theta}$
EQ ^{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 ^{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 ^{PartialSpeed}	$FA = y \cos \theta + \sqrt{z^2 - (f \cdot y \sin \theta)^2} - z$

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