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Analyzing the effect of wind on flight: pitfalls and solutions

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Summary

How flying organisms alter their air speed in response to wind is important in theories of flight energetics. Numerous studies have investigated the relationship between air and wind as a function of ground speed and air speed. This study shows that this approach can lead to erroneous results, due to spurious correlations. An alternative way to analyze air speed is proposed that overcomes the problems of one-dimensional linear models. The new model is non-linear and has two explanatory variables. Using two synthetic data sets with known properties and a data set with real observations of migratory bird tracks and wind observations, we illustrate the weaknesses of the conventional analysis as well as the strengths of the newly proposed model. This leads to the conclusion that for many studies a reanalysis of the effect of wind on air speed is desirable.

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Key words: compensation, flight, model, spurious correlation, wind.

Introduction

A fundamental aspect of flight behavior is how an organism responds to varying external factors such as wind. The relation between wind and flight behavior has important implications for migration, orientation, foraging behavior and flight energetics. Unlike many seeds, for example, that are passively dispersed by wind, intuitively we know that many flying organisms must react to wind, otherwise they would not reach their goal, whether long distance such as a wintering or breeding site, or short distance such as a foraging location. In this paper, we select birds as our topic of discussion, although many of the ideas presented below are equally relevant for insects, bats and other flying organisms. Furthermore, we focus on the analysis of air speed, but our approach can be extended to analyze heading as well. A bird's air speed and heading, movement in relation to the air, are determined by the bird's behavior, whereas ground speed and flight direction, the movement relative to the earth's surface, are determined by both the flight behavior and the corresponding winds. During powered, flapping flight a bird's air speed is directly related to the metabolic cost of flight, which can be estimated using the power curve for flight (e.g. Pennycuick, 1989; Rayner, 2001; Tucker, 1975). A bird's ground speed and flight direction are relevant for calculations of distance and duration of travel. Therefore, the relationship between wind, flight and fuel, may change with different objectives.

Numerous field and theoretical studies have tried to measure or predict how birds and insects react to wind (e.g. Liechti, 2006; Riley et al., 2003; Srygley and Oliveira, 2001). One hypothesis regarding migratory flight is that birds should maximize the distance traveled for a given amount of fuel. In order to fulfill this hypothesis birds are predicted to increase their air speeds in headwinds and decrease their air speeds in tailwinds (Liechti, 1995; Pennycuick, 1978). Pennycuick (Pennycuick, 1978) further proposed that this prediction could be tested by comparing the relationship, initially assumed to be non-linear, between air speed (V_a) and the difference between ground speed (V_g) and V_a, both scalar quantities. It is noteworthy that this difference is generally represented in the literature as V_g–V_a and termed the 'speed increment due to wind' or the 'wind effect', where positive values of V_g–V_a represent tailwinds and negative values represent headwinds. Pennycuick states "*A 'tail wind' is conventionally defined as the scalar difference between ground speed and true air speed. The 'wind effect' means that a bird whose ground speed is less than its air speed will normally respond by increasing its air speed, resulting in a negative correlation between the air speed and 'tail wind'*" [(Pennycuick, 2001) p. 3288]. Perhaps as a result of the simplicity of this particular approach, the linear relationship between V_a and V_g–V_a has been tested in the literature numerous times for birds (Alerstam et al., 1993; Alerstam and Gudmundsson, 1999; Green and Alerstam, 2000; Gudmundsson et al., 2002; Hedenström and Alerstam, 1996;

Hedenström et al., 1999; Hedenström et al., 2002; Liechti et al., 1994; Pennycuick, 1982; Pennycuick, 2001; Rosen and Hedenström, 2001; Wakeling and Hodgson, 1992) and for migratory insects (Srygley, 2003). The results have been used to determine how birds alter their air speed in relation to tailwinds and headwinds and to predict air speeds in varying wind conditions. The overwhelming evidence from these studies has often been used in support of the prediction that birds increase their air speed in a headwind and decrease their air speed in a tailwind. However, conflicting results were found when head- and tailwind situations were separated (Hedenström et al., 2002). In several cases, no relationship was found and treated as potential type II errors (Rosen and Hedenström, 2001), or no compensation for wind was made (Alerstam et al., 1993; Rosen and Hedenström, 2001). Although the initial prediction was for the specific case of pure headwind or tailwinds, the prediction was expanded to include the influence of side wind on optimal air speeds (Liechti et al., 1994); however, no solution was provided for analyzing the effects of side and tail winds simultaneously.

Both wind and flight are composed of two components that can be considered either in the form of speed and direction or in the form of their x and y vector components for a given coordinate system. If the influence of wind on flight is studied in only one of these two dimensions while either speed or direction vary, information is lost and erroneous interpretations may result. To our knowledge, all studies investigating the influence of wind on heading (e.g. Srygley, 2003; Srygley et al., 1996; Wege and Raveling, 1984) or air speed (e.g. Able, 1977; Alerstam et al., 1993; Hedenström et al., 2002; Pennycuick, 2001) have adopted a one-dimensional model. With a one-dimensional model we mean a model with only one explanatory variable. In this paper we will focus on the analysis of air speed. We argue that the conventional analysis of air speed in relation to wind, by testing the linear relationship between the scalar V_a and $V_g–V_a$, cannot be used to assess the relationship between air speed and wind nor, more specifically, the prediction that birds should maximize the distance traveled per fuel cost by increasing their air speeds in headwinds and decreasing it in tailwinds. This paper provides an alternative approach to test how birds alter their air speed in relation to wind speed and direction. Three different datasets are used to illustrate the weakness of the conventional model as well as the strengths of the newly proposed model for (1) simulated random data, (2) simulated artificial data including an established influence of wind and (3) measured autumn passerine migration and corresponding wind conditions.

Materials and methods

In this section we first provide some definitions and describe the basic mathematical properties of the system that we are studying. This is followed by an explanation of the conventional analysis of the effects of wind on a bird's air speed, as well as a new method of analysis. Then, we describe the analytic framework we use to test the two methods, and finally we describe the data sets that we used in our testing procedure.

The relation between vector components, speed and direction

To study bird flight in relation to wind, we need three orthogonal vectors. The first expresses a displacement per unit time of the bird with respect to the ground (we will call this the ground vector, **g**) the second vector expresses the displacement of the bird with respect to air (the air vector, **a**) and the third expresses the displacement of the wind (the wind vector, **w**). In this study we consider movement in the horizontal plane and ignore vertical movement, hence our vectors have two elements only: displacement in the x- and y-directions. Fig. 1 gives a graphic representation of this system, and the three vectors are defined as follows:

$$\mathbf{g} = \begin{bmatrix} x_g \\ y_g \end{bmatrix},\ \mathbf{a} = \begin{bmatrix} x_a \\ y_a \end{bmatrix},\ \mathbf{w} = \begin{bmatrix} x_w \\ y_w \end{bmatrix}. \quad (1)$$

In this study we have chosen to represent the eastern direction by positive x and the northern direction by positive y. The lengths of these vectors are scalars and are known as ground speed (V_g), air speed (V_a) and wind speed (V_w). These are calculated as follows:

$$V_g = \sqrt{x_g^2 + y_g^2}\ , \quad (2a)$$

$$V_a = \sqrt{x_a^2 + y_a^2}\ , \quad (2b)$$

$$V_w = \sqrt{x_w^2 + y_w^2}\ . \quad (2c)$$

Angles between the vectors and some reference direction can also be conveniently calculated on the basis of the x and y components, using the following equations:

$$\gamma = \arctan(x_g/y_g)\ , \quad (3a)$$

$$\alpha = \arctan(x_a/y_a)\ , \quad (3b)$$

$$\omega = \arctan(x_w/y_w)\ . \quad (3c)$$

Here γ is known as the track direction, α the bird's heading and ω the wind direction. We have chosen to define north as the zero angle. Following from the definition of positive x and y in the eastern and northern directions respectively, the angles are positive in the clockwise direction.

Obviously, the three vectors are not independent: the ground vector is the sum of the air and wind vectors:

$$\mathbf{g} = \mathbf{a} + \mathbf{w} \leftrightarrow \begin{bmatrix} x_g \\ y_g \end{bmatrix} = \begin{bmatrix} x_a + x_w \\ y_a + y_w \end{bmatrix} = \begin{bmatrix} x_a \\ y_a \end{bmatrix} + \begin{bmatrix} x_w \\ y_w \end{bmatrix}. \quad (4)$$

In most studies, air speed (V_a) and heading (α) are not measured directly, nor are the x- and y-components. Rather, ground speed (V_g) and direction (γ) and wind speed (V_w) and direction (ω) are measured. Note that when studying the influence of wind on flight, we are interested in the direction wind is blowing to. Wind measurements received from climatological surface

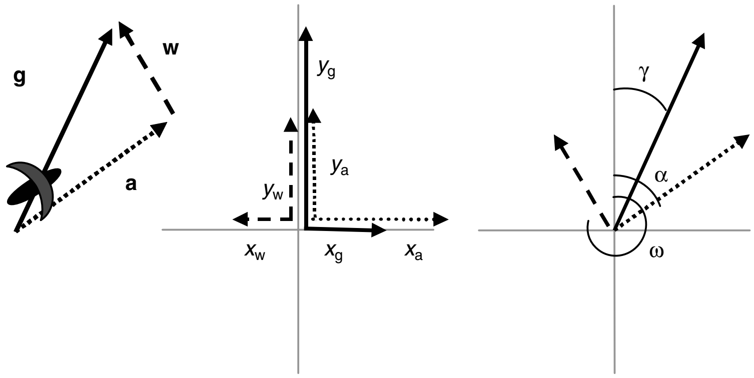

Fig. 1. A graphic representation of the relationship between **a**, **g** and **w**, the orthogonal components x_a, y_a, x_g, y_g, x_w, y_w, α (heading), γ (track or ground direction), ω (wind direction).

stations often note meteorological wind direction, which is the direction wind is blowing from.

On the basis of the available information, V_a and α can be calculated. It is convenient to first calculate x_a and y_a:

$$\left.\begin{array}{l} x_g = V_g \sin(\gamma) \\ y_g = V_g \cos(\gamma) \\ x_w = V_w \sin(\omega) \\ y_w = V_w \cos(\omega) \\ \begin{bmatrix} x_a \\ y_a \end{bmatrix} = \begin{bmatrix} x_g - x_w \\ y_g - y_w \end{bmatrix} \end{array}\right\} \rightarrow \begin{bmatrix} x_a \\ y_a \end{bmatrix} = \begin{bmatrix} V_g \sin(\gamma) - V_w \sin(\omega) \\ V_g \cos(\gamma) - V_w \cos(\omega) \end{bmatrix}. \quad (5)$$

The heading α can then be calculated by applying Eqn 3b.

Air speed is finally obtained by applying Eqn 2b using x_a and y_a calculated in Eqn 5. Although apparent from Eqn 4, it is important to note at this point that any four out of the six variables determine the values of the other two. For clarity we also show the full expression for V_a as a function of V_g, γ, V_w, ω in Eqn 6:

$$\begin{aligned} V_a &= \sqrt{[V_g \sin(\gamma) - V_w \sin(\omega)]^2 + [V_g \cos(\gamma) - V_w \cos(\omega)]^2} \\ &= \sqrt{V_g^2 + V_w^2 - 2V_g V_w [\sin(\gamma)\sin(\omega) + \cos(\gamma)\cos(\omega)]} \\ &= \sqrt{V_g^2 + V_w^2 - 2V_g V_w \cos(\gamma - \omega)}\,. \end{aligned} \quad (6)$$

With Eqn 6 in mind we can review the relation between V_a and (V_g–V_a), whose linear relationship has been tested to detect a negative slope in avian and entomological literature (see Introduction):

$$V_a \propto (V_g - V_a)\,. \quad (7)$$

By substituting Eqn 6 in Eqn 7, Eqn 7 becomes a rather complex implicit relation. In this context, implicit means that V_a occurs at both the right and left hand side of the equation. The linearity hypothesis, expressed by Eqn 7, is not valid in general, since $nV_a \neq n(V_g - V_a)$. The functional relationship between V_a and (V_g–V_a) depends on V_g and V_w as well as on γ and ω and is generally not linear as often treated in the literature (Fig. 2 and Fig. S1 in supplementary material).

Two special situations can be distinguished where Eqn 7 is applicable and the relationship between V_a and V_g–V_a is linear. The first is when V_g is constant. Then the relation will be a line with slope –1 and intercept V_g (i.e. $V_a = a - V_a$, with $a = V_g$). The second situation occurs when (γ–ω)=0 or (|γ–ω|)=180°, a pure tail- or headwind, respectively, with respect to the ground vector (see Fig. 2A for pure tailwind). In this case, $V_a = V_g - V_w$; note that although this is quite obvious, it also follows from Eqn 6 by setting cos(γ–ω) to 1, and subsequently factoring the equation. This equality implies that V_g can be eliminated in Eqn 7 so that one obtains a function with only V_w as explanatory variable ($V_a = a + bV_w$). Clearly, many different functional relationships between V_a and V_g–V_a may be expected, including positive relationships, for example, with pure side winds in respect to the ground vector and fairly constant wind speeds (Fig. 2C). To provide intuitive insight in the relation between V_a and V_g–V_a, the two-dimensional relation between **g**, **a** and **w** is depicted for a few points from Fig. 2B (Fig. 3).

In Fig. 4 we further illustrate the relation between V_a and V_g–V_a with randomly generated data. Here only the cases with *ω*–*γ*=45° and *ω*–*γ*=135° are shown. In this example, V_g and V_w are independently generated random variables with a mean of 10 m s^{-1}. The variance of V_w equals 4 m^2 s^{-2} and the variance of V_g equals 0, 1 and 4 m^2 s^{-2} (Fig. 4, top to bottom). V_a is calculated on the basis of V_g, γ, V_w and ω. As previously described, when V_g is constant, the relation between V_a and V_g–V_a is a straight line with slope –1. However, if V_g varies, the amount of correlation decreases, depending on ω–γ as well as the variability of V_g relative to that of V_w.

Methods to investigate speed changes under influence of wind

We apply the conventional method to investigate the influence of wind on air speed to test for the significance of the relation $V_a = a + b(V_g - V_a)$. Despite the problems with this method as explained above, we fit it to several data sets in order to compare the results with the alternative method we propose. For this model we use the *T*-statistic to test whether the predictor explains a significant proportion of the variance. We then review the residual plots and the quantile–quantile plots to evaluate the normality assumptions underlying the linear model. The R^2 statistic is used to determine the overall fit of the model.

As a more appropriate method of analysis we propose a two-dimensional model. Our method departs from the fact that V_a is, by definition, a function of two variables, so any model for V_a will have to be explicit (V_a only on the left hand side of the

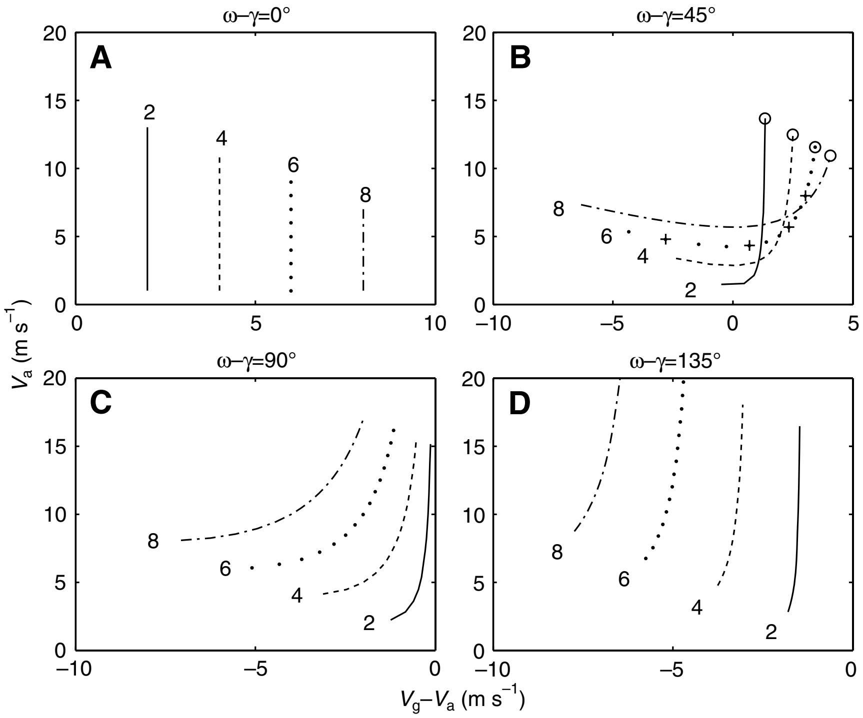

Fig. 2. The relation between V_a and V_g–V_a for different combinations of V_w and ω–γ (A, ω–γ=0°; B, ω–γ=45°; C, ω–γ=90°; D, ω–γ=135°). In each subplot V_g varies from 1–15 m s^{-1}, and the isoclines represent constant V_w (2, 4, 6, 8 m s^{-1}). Note that A represents pure tailwind conditions and C represents pure side winds in relation to the ground vector. To ensure a biologically realistic representation, A is constrained as follows: V_g>V_a and V_g>V_w. In B, circles represent constant V_g (15 m s^{-1}) and a varying V_w (2,4,6 and 8 m s^{-1}), + symbols represent constant V_w (6 m s^{-1}) and varying V_g (2, 5, 8 and 11 m s^{-1}), see Fig. 3 for the individual vectors. See Fig. S1 (supplementary material: online appendix) for animated 3-D visualizations of these figures.

equation) and two-dimensional. Secondly, we search for orthogonal variables to make maximum use of the information content in a dataset when fitting our model. In the third place, we try to specify variables that are meaningful in a physical or biological sense. Finally we try to use a modeling framework that is statistically well developed and offers large flexibility to model linear as well as non-linear systems.

The modeling framework that provides the flexibility that we are looking for is a generalized additive model [GAM; see Guisan et al. (Guisan et al., 2002), and references therein]. For this model we use the χ^2 statistic to test whether a predictor explains a significant proportion of the variance and other graphical diagnostics are used to evaluate the performance of a model such as residual plots, quantile–quantile plots and Cook's distance to identify potential outliers. In a GAM, deviance reduction is used as a measure of model fit and the adjusted D^2 value (comparable to the adjusted R^2), which takes into account the number of predictors and observations, is used to determine the real fit of the model and to compare models (e.g. Guisan and Zimmermann, 2000).

Two orthogonal variables that are related to V_a and have no implicit relationship with V_a, or V_g, are the components of wind along the *x* and *y* axis. The two variables are implemented in a GAM by first transforming them *via* a rather constrained LOESS smoother (a locally weighted regression) with a maximum span of 80% and 1–2 degrees of freedom (d.f.) (Cleveland, 1979; Cleveland and Devlin, 1988). The resulting GAM then has the following form:

$$V_a = f(x_w) + f(y_w)\,, \quad (8)$$

where the function *f*() refers to the transformation *via* a LOESS smoother. If the transformation is not justified, after initial model derivation, then variables are maintained in their linear form.

Testing both analyses

In this study we test the two analyses by performing an experiment using data sets with known properties. A first data set is generated with no relation between the air vector and wind vector at all (SRD, simulated random data), therefore no wind compensation. A second data set is generated with a very strong relation between the air and wind vectors (SWI, simulated wind influence), to represent full wind compensation. The two analyses are applied to both data sets. A correct analysis should obviously identify both situations correctly.

Both methods are also applied to real data (a situation where the degree of compensation is unknown) to consider the different conclusions from both methods with respect to the real data.

Description of the data sets

Data set SRD, simulated random data, was generated to comprise 880 artificial data records of bird flight and wind. The wind components (x_w and y_w) were generated independently with a pseudo random number generator, using a Gaussian process with a mean of 0 m s^{-1} and a standard deviation (s.d.) of 4 m s^{-1}. Similarly, x_a and y_a were generated independently using a Gaussian process with a mean of 0 m s^{-1} and s.d.=3 m s^{-1}. Therefore, all four components are entirely independent of each other and we should not find any relationship between wind components and flight components. The ground vector is generated as the sum of the air and wind vectors (*viz*. Eqn 4).

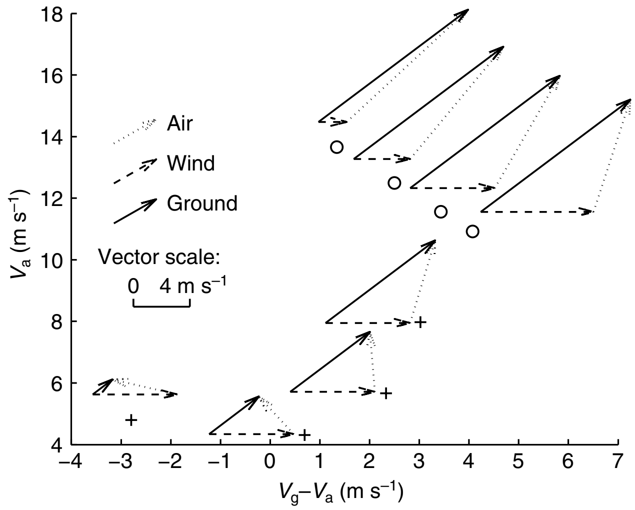

Fig. 3. The relation between V_a and V_g–V_a where ω–γ=45° expressed in vectors. Circles represent constant V_g (15 m s^{-1}) and a varying V_w (2,4,6 and 8 m s^{-1}), + symbols represent constant V_w (6 m s^{-1}) and varying V_g (2, 5, 8 and 11 m s^{-1}). All the points shown here are subsets of those in Fig. 2B.

A second data set SWI, simulated wind influence, was created to represent a strong influence of wind on V_a and α. The dataset contains 880 artificial data records of birds that adjust V_a and α to maintain constant V_g and γ while winds are variable. The ground components were chosen to be x_g=6 m s^{-1} and y_g=3 m s^{-1}, with a small Gaussian noise added (using a mean of 0 m s^{-1} and a s.d.=1 m s^{-1}). The x_w and y_w components were taken from the SRD data. The x_a and y_a components were subsequently calculated by x_g–x_w and y_g–y_w and finally V_g and V_a were calculated (Eqn 2a, 2b).

The third dataset was taken from a radar field study in southern Germany [for measurement details, see Liechti (Liechti, 1993)]. The data set contains 880 radar tracks of autumn passerine migration (APM) with direct observations of V_g, γ, V_w and ω. V_a was computed from these using Eqn 6.

Rose plots of the headings and direction of flight for all three data sets are shown in Fig. 5.

Results and discussion

The conventional approach, a one-dimensional linear model

We tested the relationship between V_a and V_g–V_a for three different datasets (Fig. 6.). From the structure of the simulated random data (SRD) we know that there is no relationship between the wind and air components of flight, all variables are independent. Therefore, the negative slope in Fig. 6A, although marginally statistically significant (R^2=0.06, P<0.001), is the result of a spurious correlation between V_a and V_g–V_a. On the other hand, the negative slope in Fig. 6B, the simulated wind influence (SWI), reflects a true negative relationship between air speed and (V_g–V_a) (R^2=0.94, P<0.001). In the SWI dataset, the birds make the necessary adjustments in air speed and heading to fully compensate for the winds and maintain constant ground speed and heading. Because ground speed is constant, the SWI example is one of the special cases where Eqn 7 is applicable. With these examples we have now illustrated that spurious correlations appear if one takes uncorrelated and random data for V_a and V_w. Therefore, although there is a significant negative relationship for the

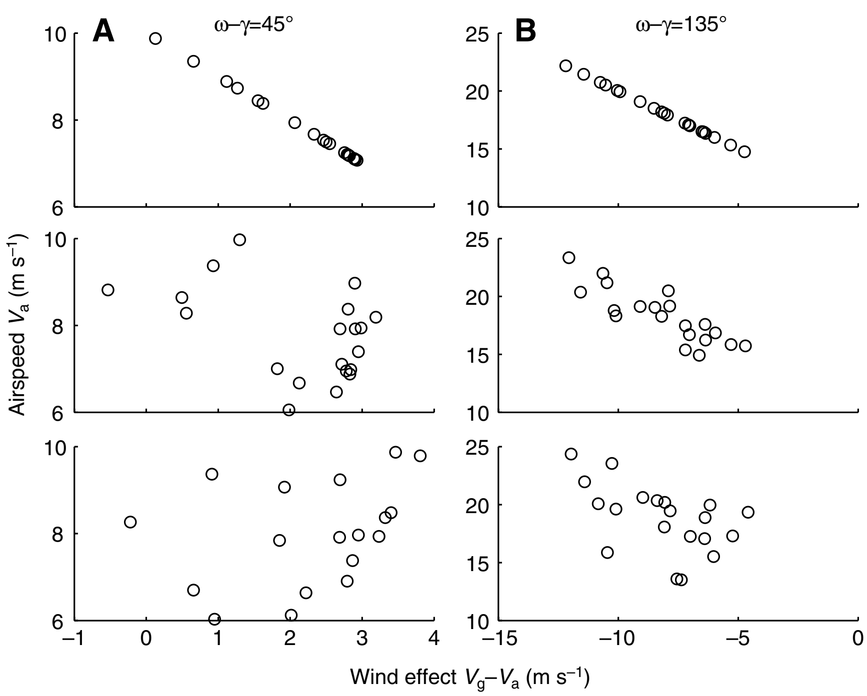

Fig. 4. An illustration of the correlations that arise in random V_g and V_w data as a function of variance V_g/variance V_w and ω–γ. (A) ω–γ=45°, (B) ω–γ=135°. In all cases, the variance of V_w=4 m^2 s^{-2}. In the top row, V_g does not vary. In the second row, variance of V_g=1 m^2 s^{-2} and in the bottom row, variance of V_g=4 m^2 s^{-2}. V_a is calculated on the basis of V_g, γ, V_w and ω.

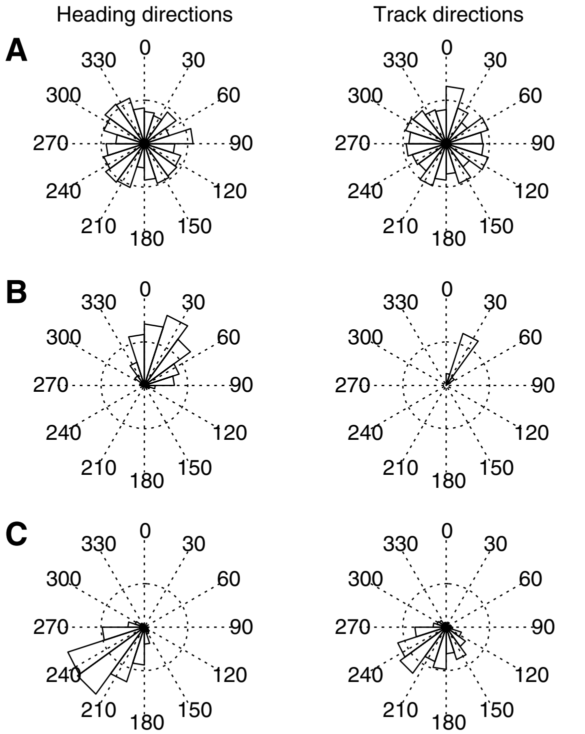

Fig. 5. Rose plot histogram of flight heading (left) and track direction (right) for each data set as follows (A) SRD (simulated random data), (B) SWI (simulated wind influence), (C) APM (autumn passerine migration). Note that 0° direction depicts north in our analysis (y>0) and 90° depicts east (x>0).

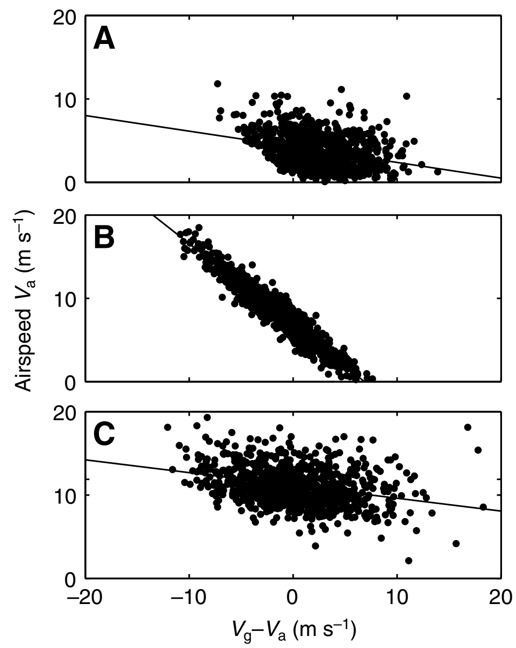

Fig. 6. Graphical representation of traditional test of the influence of wind on air speed (V_a in relation to V_g–V_a). Three data sets were used (A) SRD (simulated random data; no relation between wind and flight) (B) SWI (simulated wind influence) (C) APM (measured autumn passerine migration dataset). In each dataset N=880.

migration dataset (APM) between V_a and V_g–V_a using the conventional approach (Fig. 6C, R^2=0.10, P<0.001), it provides no evidence for a biologically meaningful relationship between V_a and wind. Clearly, from these examples, an alternative analysis is necessary to determine if there is a biologically significant relationship between wind and air speeds.

Analyzing air speed in two dimensions, as a function of the x and y wind components

As expected, there is no statistically significant relation between V_a and x_w, y_w for the simulated random data (SRD, Table 1) when applying either a GAM (Fig. 7A) or a linear model. On the other hand, with the SWI dataset V_a is significantly related to x_w and y_w (Fig. 7B, Table 1). Both components of wind are equally influential on V_a. V_a increases as wind along the x-axis decreases or increases from 6 m s^{-1} and decreases or increases from 3 m s^{-1} along the y-axis. In other words as winds increasingly deviate from the ground speed and direction (x_g=6 m s^{-1}, y_g=3 m s^{-1}), V_a increases. For complete wind compensation, where V_g and γ are constant, the local minima of each variable indicate the mean ground vector (x_g, y_g). Thus, by applying a GAM, we find the true constant x_g, y_g values.

For the observed autumn passerine migration (APM) the final model shows only a marginal linear influence of wind on V_a (Table 1). This model was derived as follows. First a GAM was applied on the LOESS transformed wind components (x_w, y_w) (Fig. 7C). However, the LOESS transformations of both variables were not significant. A linear model was then fit for both variables. In this model, y_w appeared to be insignificant, hence it was excluded.

In the final model, V_a is only slightly influenced by wind along the x-axis. As winds blow more strongly towards the east, birds increase V_a, whereas birds decrease V_a when winds blow to the west (Fig. 7C). As tracks and headings are mainly towards SW (Fig. 5C), the x-component includes a tailwind as well as a side wind component. Although birds appear to increase air speed in headwinds and decrease in tailwinds when applying the conventional analysis, this relationship does not emerge when considering both wind components.

Conclusions

One question addressed by many biologists is: how do flying organisms adapt their flight behavior to dynamic wind conditions? By way of an artificial analytical example we have illustrated that the conventional approach to test the hypothesis that birds maximize their distance per energy consumption by increasing their airspeed in headwinds and decrease their airspeed in tailwinds is incorrect. The negative relationship between V_a and V_g–V_a can result from spurious correlations in the data. The two reasons for this spurious correlation are that: (1) V_a is not only a function of V_g–V_a but also a function of V_w

Table 1. *Models for predicting air speed as a function of the wind components along the x and y axes (x_w and y_w respectively)*

Dataset	Model structure	Adjusted D^2	P-value
SRD	V_a~$lo(x_w, 0.8, 2)+lo(y_w, 0.8, 2)$	NS	NS
SWI	V_a~$lo(x_w, 0.8, 2)+lo(y_w, 0.8, 2)$	0.91	<0.001
APM	V_a~$0.09x_w+10.8$	0.07	<0.001

V_a, air speed; x_w, y_w, wind components along the *x* and *y* axes, respectively; SRD, SWI and APM, simulated random data, simulated wind influence and the measured autumn passerine migration datasets, respectively.

The parameters included in each model are significant ($P<0.05$), except for the SRD dataset where none of the parameters are significant (NS, not significant). *lo*() is the LOESS smoother function with the variables, span and degrees of freedom in parentheses. Adjusted D^2 is a measure of deviance reduction and model fit.

and ω–γ; (2) V_a depends non-linearly on these variables; a linear model is only applicable with constant ground speed or pure head/tailwind conditions. Alternative general forms of analyses, that encompass the multidimensional and non-linear nature of wind and flight, are necessary.

Our approach, a two-dimensional generalized additive model, provides a simple, general and straightforward method to analyze the complex relation between air speed and wind speed and direction without the risks entailed in information reduction. In this study the new approach was tested on both synthetic and observed data. Similarly, this approach can be applied to studying the relationship between heading, rather then air speed, and both wind components. Although other studies have described the importance of multidimensional analysis (e.g. Green and Alerstam, 2002; Liechti et al., 1994) a general approach to studying the influence of wind speed and direction simultaneously on air speed has not been suggested. See however Shamoun-Baranes et al. (Shamoun-Baranes et al., 2003), who applied a GAM to study the influence of the tailwind and side wind component simultaneously on ground speed.

The analytical problems associated with the simplification of observational data are a recurrent issue in biology (e.g. Jackson, 1997) and can have serious consequences for the

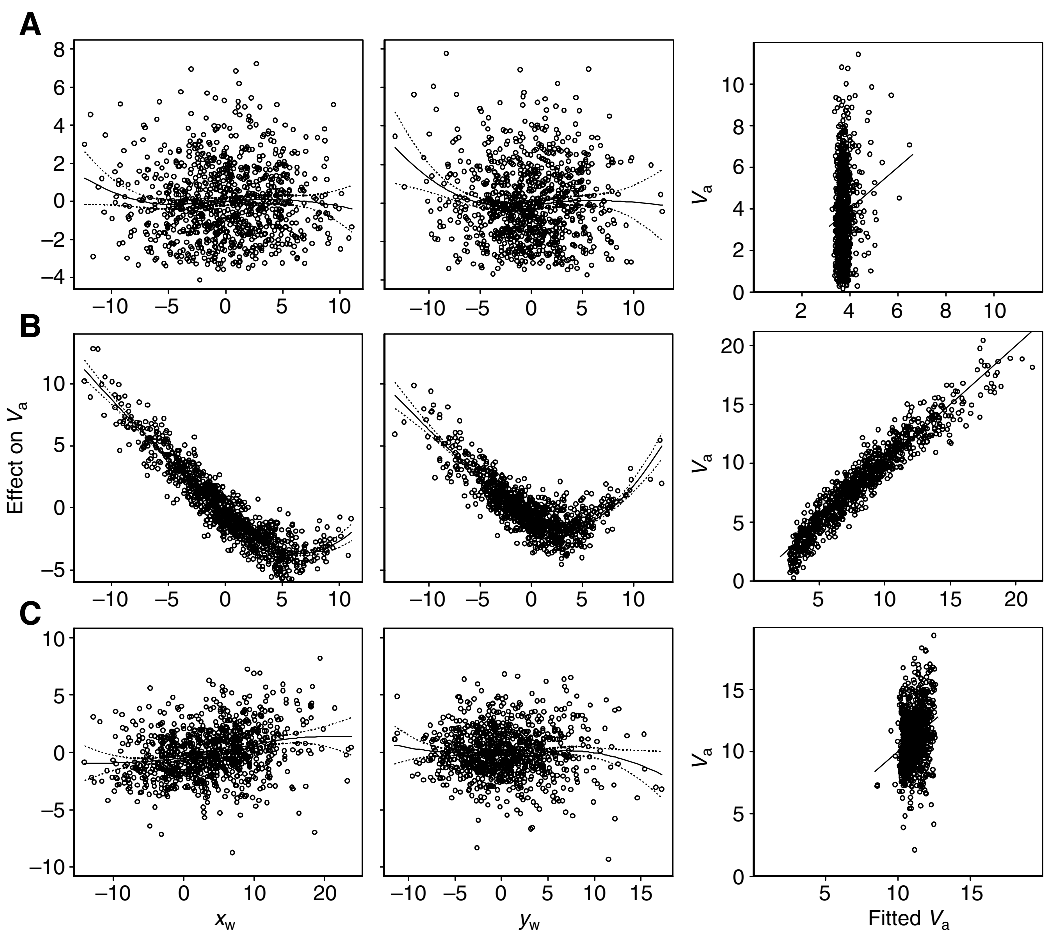

Fig. 7. The predicted relative influence of the wind components (x_w and y_w, left and center respectively) on air speed (V_a) for each dataset (A) SRD (simulated random data; no relation between wind and flight) (B) SWI (simulated wind influence) (C) APM (autumn passerine migration). The form of each GAM is V_a~$lo(x_w, 0.8, 2)+lo(y_w, 0.8, 2)$. The *y*-axis represents the contribution of x_w and y_w on V_a. The solid line is the fitted functional response and the broken lines represent the 2× standard error curves, the circles represent the partial deviance for each observation point. The local minima in Fig. 7B correspond with x_g (6 m s^{-1}) and y_g (3 m s^{-1}) in the SWI dataset. Figures on the far right represent the observed (*y*-axis) *vs* fitted V_a (m s^{-1}) (*x*-axis); note that the *x* and *y* axis are not always equally scaled.

foundations of our theories. The broadly accepted analysis of air speed and wind discussed in this paper has not only been used to support the current theories on optimal avian flight but also to form them. The validity of these and other one-dimensional studies in their current form may therefore also influence our theoretical foundations. Hence, a reanalysis of previous one-dimensional studies dealing with the effect of wind on air speed is desirable. The adaptive behavior of birds towards their environment, particularly wind, has important implications when incorporated into models of, for example, stopover strategies and take-off decisions during migration (Liechti and Bruderer, 1998; Weber et al., 1998; Weber and Hedenström, 2000) estimations of potential flight range of long distance migrants (Battley and Piersma, 2005), of optimal flight speeds of birds (Hedenström and Alerstam, 1995), energetic requirements during for migration (Butler et al., 1997) consequences for individual fitness (Clark and Butler, 1999) and the evolution of migratory strategies (Erni et al., 2005). In order to properly interpret model results or compare models to measurements we must ensure that the analysis underlying model assumptions or the predictions themselves is appropriate.

We hope this paper stimulates new and revisited studies of the influence of wind on flight.

List of symbols

a	air vector
APM	autumn passerine migration
g	ground vector
GAM	generalised additive model
lo	LOESS smoothing function
SRD	simulated random data
SWI	simulated wind influence
V_a	air speed
V_g	ground speed
V_w	wind speed
w	wind vector
α	bird's heading
γ	track direction
ω	wind direction

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