Investigating wind effects on insect migration

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Abstract

Understanding the response of migrating insects to the wind along their path is an active area in insect migration research. In this article, two methods for describing wind response are illustrated and evaluated by analysing a model of migratory movement with a realistic scatter in the flight direction. The results show that both methods give robust and reliable results when insects simply maintain a constant heading in response to winds with a cross track component. However, neither method is reliable for evaluating whether insects are compensating for wind drift and maintaining a constant track towards their destination.

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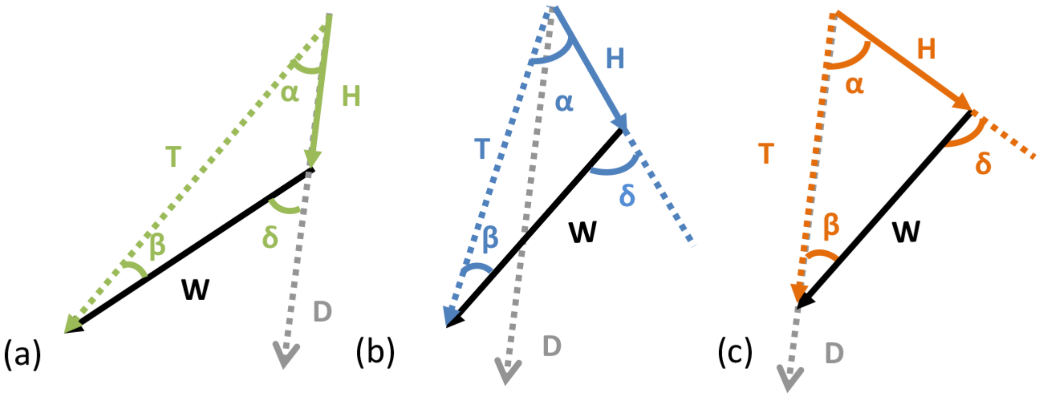
1 Introduction

Insects may undertake seasonal migrations between locations that are hundreds, or even thousands, of kilometres apart, but the strategies they use to determine their flight orientation are poorly understood. It is known that migratory insects show a range of responses to wind; Chapman et al. [1] identified six possible strategies based on the direction of their movement relative to the wind and to the destination direction. Among these, the four most important strategies are: compass-biased downwind orientation, for which an insect deviates its heading slightly from the downwind to lie between the wind and the destination; full drift, for which it does not change its initial heading, regardless of the wind direction (Figure 1(a)); complete compensation, for which it adjusts its initial heading to maintains its course towards the destination (Figure 1(c)); and partial compensation (or partial drift) for which its heading lies between full drift and complete compensation

Figure 1: The triangle of velocities for three different situations: (a) full wind drift; (b) partial drift (or partial compensation); (c) complete compensation. Here, **T** is the track vector, the insect's flight direction and speed over the ground; **H** is the heading vector, the insect's flight direction and speed relative to the air; ***W*** is the wind vector, the wind direction and speed at the height the insect flies; **D** is the direction to the insect's migration destination; β is the angle between the track and wind direction; δ is the angle between the heading and wind direction; and $\alpha = \delta - \beta$ is the angle between the track and heading.



(Figure 1(b)) and the track direction is closer to the destination than in full drift but not close enough to completely compensate for the effect of wind [1].

There are several studies of drift and compensation in insect migration. Previous work in Europe demonstrated that some butterflies and large moths are not always passively advected by the wind, but use a crosswind heading to optimise their flight trajectories [2, 3, 4]. Do insects migrating in inland Australia show similar behaviour? Before attempting to answer this question, it is appropriate to examine the proposed analysis methods with simulated data to determine their effectiveness and reliability for insects, which have lower air speeds than the birds for which the methods were developed.

In this article, we investigate two methods that were used in bird migration studies [5] and determine, via quantitative estimates, whether migrants are drifting with, or compensating for, the winds at their flight altitude. As in the study by Green and Alerstam [5], both methods are analysed using a model for migratory movement with a realistic scatter in the flight directions, for the ideal case of full drift and complete compensation. In the analysis, we use information about the insects' air speeds, derived from the combination of radar observations and wind fields computed with an atmospheric model, to provide typical values of the bounds on the possible ratio of the wind speed to the flight speed of the insects. This ratio is much larger for insects than for birds, and there are limiting situations for full wind drift and complete compensation that do not arise in the bird case.

2 Method

2.1 Research tools and data

We use entomological radar data from Bourke, NSW over three years from 2006 to 2008 and for heights between 175 and 1300 m above the ground. The radar observations include the insects' flight altitude, their track directions and speeds of travel relative to the ground (track vector $\mathbf{T}$), and their compass orientation (heading direction). The Air Pollution Model (TAPM) [6], developed by the CSIRO, was used to simulate the wind directions and wind speeds (wind vector $\boldsymbol{W}$) at the heights the insects were flying. The air speed is derived from the vector subtraction of the radar-observed track vector $\mathbf{T}$ and the modelled wind vector $\boldsymbol{W}$. In the analysis, Australian plague locusts (*Chortoicetes terminifera*) are classified based on the character of their radar returns [7], and their air speeds are used to estimate the ratio of the wind speed to the insects' air speed for use in the model. Locusts were detected at different times at all the heights that the radar covers.

TAPM was tested both in Australia and overseas [8], and Taylor et al. [9]

verified the model by comparing the simulated upper winds at Wagga Wagga, NSW with observations from a sodar and an electromagnetic wind profiler. We also compare surface winds and other meteorological variables from the model with observations from automatic weather stations at Bourke and six nearby sites. Overall, TAPM demonstrates root-mean-square (rms) errors for predicted wind speed that are significantly less than typical insect flight speeds.

2.2 Triangle of velocities

As illustrated by the triangles of velocities shown in Figure 1, an insect's movement over the ground, that is, its track direction and ground speed $\mathbf{T}$, is the vector sum of its heading direction and air speed $\mathbf{H}$ and the wind vector $\boldsymbol{W}$. We assume a preferred direction of movement $\mathbf{D}$, and identify several possible movement strategies (Figure 1), including two basic cases of full wind drift (Figure 1(a)), and complete compensation (Figure 1(c)).

Green and Alerstam [5] showed that if an insect migrates towards a fixed heading direction with constant air speed (full wind drift), then its track will vary relative to the wind by

$$\alpha = \arctan\left(\frac{a \sin \delta}{1 + a \cos \delta}\right), \tag{1}$$

where a is the ratio of the wind speed to the animal's air speed and the angles α, β, and δ are as defined in Figure 1. On the other hand, when the insect migrates along a fixed track with constant air speed (complete compensation), its heading will vary in different wind conditions according to

$$\alpha = \arcsin(a \sin \beta)\,. \tag{2}$$

For birds, the ratio a in equations (1) and (2) is typically less than one; however, for insects it is often greater than one, and this limits the situations where the insect can undertake complete compensation. The ratio also limits a fully drifting insect's ability to fly to its destination. If insects adopt a full drift strategy, or they are unable to fully compensate, then they may be carried away from their destination.

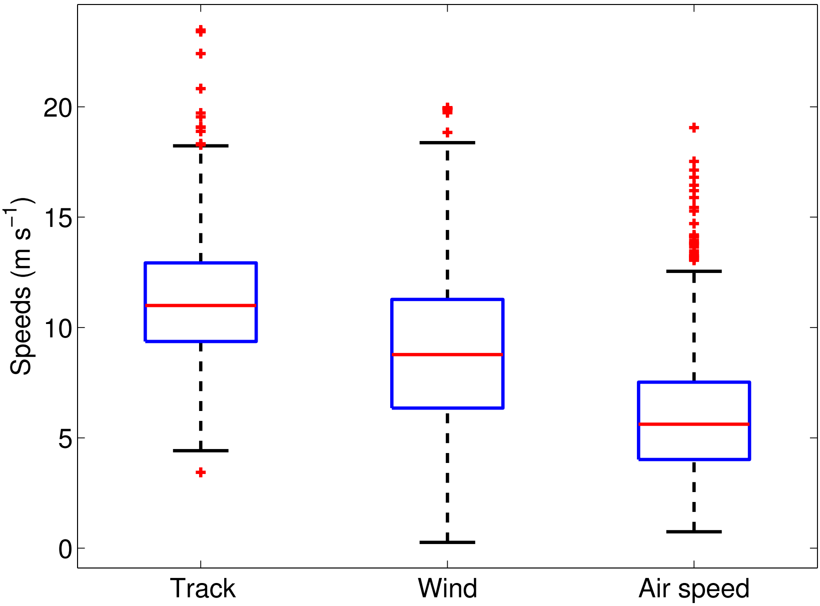
When $a > 1$, that is, the insects' air speed is less than the wind speed, it follows from equation (2) that complete compensation can only be achieved when $\beta < \arcsin(1/a)$, while with full wind drift, movement towards the destination requires $\alpha < 90^\circ$, and thus from equation (1), $\delta < 180^\circ - \arccos(1/a)$. In the special case of $a = 1$, complete compensation can only be achieved if the angle between the preferred direction and the wind $\beta < 90^\circ$, and for the case of full wind drift, $\delta \neq 180^\circ$ (if $\delta = 180^\circ$, then the insects will make no progress, that is, $|\mathbf{T}| = 0$). For $a < 1$, no limitation applies in either case; however, while movement towards the destination direction may be possible, it may be very slow.

Analysis of radar track data and modelled winds for Australian plague locusts at Bourke suggest that the ratio of the mean wind speed to mean air speed $a = 1.5$ (Figure 2). With changes in wind speed, a will vary considerably from night to night, thus we use the ratios $a = 1.5$ as the mean value, $a = 1.8$ and $a = 1.3$ to sample the normal range of a, and $a = 1$ as it is a special case. When the ratio is 1.5, insects experiencing full drift will be carried away from their destination unless the angle between goal direction and the wind direction $\delta < 132^\circ$ (Figure 3(a)). Complete compensation can only be achieved when the angle between the goal direction and the wind direction $\beta < 42^\circ$ (Figure 3(b)).

2.3 Evaluating methods for analysing drift

To estimate the insects' drift or compensation strategies we investigated two methods that were used for bird migration [5].

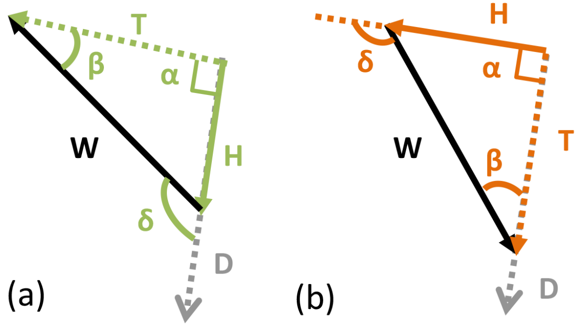
Figure 2: Box plots over three autumns for: track speeds of locusts from radar data; wind speeds from TAPM data at the height locusts fly; and the locusts' air speeds. In each box, the central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the 99.3% coverage if the data are normally distributed, and outliers are plotted individually as red crosses.



2.3.1 Regression method

The mean geographic track and heading directions for the migratory events in different wind situations are regressed on the angle α. In this method, b_{track} is the regression slope for the relationship between the track direction and α, and b_{head} is the regression slope for the relationship between the heading direction and α. Following Green and Alerstam [5], we both average over 10° intervals in wind directions, and separate the wind directions into six sectors: tailwinds from the left and right sides (45° sectors), crosswinds from

Figure 3: The limiting cases for: (a) full wind drift, when insects are moving away from their destination with $\alpha > 90^\circ$; and (b) complete compensation, when insects are unable to achieve tracks coincident with the goal direction if β is increased. The figure is drawn for the ratio $a = 1.5$.



the left and the right sides (90° sectors), and headwinds from the left and the right sides (45° sectors) in relation to the mean track direction. Then each group of α and the tracks or the heading directions are averaged and the means for each group are used in the regression to calculate b_{track} and b_{head}.

It is deduced that $b_{\text{head}} = b_{\text{track}} - 1$ as α is the angle between the track and heading (track minus heading) [5]. For the full wind drift situation, $b_{\text{head}} = 0$ since the heading directions remain constant relative to α and hence $b_{\text{track}} = 1$. For the case of complete compensation, the track directions remain constant so that $b_{\text{track}} = 0$ and $b_{\text{head}} = -1$. In Section 3, all these deductions are tested by our mathematical model.

2.3.2 Comparison method

The mean track and heading directions of a migratory event are compared in situations where the winds are coming from different sides relative to the mean track. The significance of differences in the tracks and headings in winds coming from the left and right sides are tested using the Watson–Williams test [10]. This method gives an estimate of the magnitude of drift according to

$$b_{\text{track}} = \frac{T_1 - T_2}{\alpha_1 - \alpha_2}\,, \tag{3}$$

$$b_{\text{head}} = \frac{H_1 - H_2}{\alpha_1 - \alpha_2}\,. \tag{4}$$

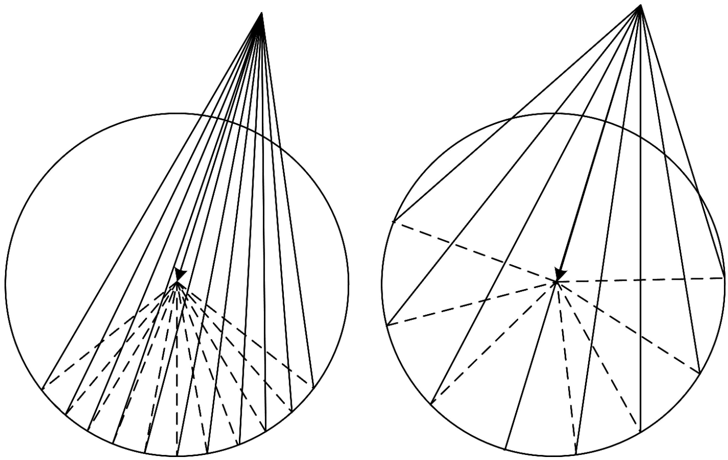
In the calculation, T_1 and T_2 denote mean track directions with winds from the left and right sides, and corresponding headings are H_1 and H_2. Then $\alpha_1 = T_1 - H_1$ and $\alpha_2 = T_2 - H_2$.

The comparison method is an alternative to the regression method which, as we show in Section 3, gives a simple graphical picture of the insects' response to winds. For the comparison method, rather than coming directly from the regression analysis, confidence intervals for the slopes b_{track} and b_{head} need to be computed by propagating the uncertainties in T_1, T_2, H_1, H_2, α_1 and α_2.

To investigate the regression and comparison methods in an ideal situation, following Green and Alerstam [5], we set up a simple model of an insect migration. In a real insect migration, variability within the population is likely to cause the insects to exhibit a range of headings in the full wind drift situation, and a range of preferred directions will manifest as a range of tracks in the case of complete compensation. We model an insect's migratory movement with a uniform spread of directions $\pm 50°$ around the mean direction (taken arbitrarily to be towards $180°$, i.e., due south) under the two conditions of full drift (Figure 4(a)) and complete compensation (Figure 4(b)).

Using equations (1) and (2), we solve the triangle of velocities for each $10°$ of the heading directions (in the case of full wind drift) or the track directions (in the case of complete compensation). We repeat these calculations for each $10°$ of the wind directions around the full circle, resulting in a total of 36 different wind conditions. For the case of full wind drift, when $a > 1$, with 11 flight directions in 36 wind conditions, the total number of trigonometric calculations is 396, while the number is 385 when $a = 1$ since there is no track vector when the heading directions and the wind directions are opposite.

Figure 4: Two instances with wind towards $200°$ for (left) full wind drift, and (right) complete compensation. A circle with radius equal to the insects' air speed (broken lines) is drawn from the head of the wind vector (arrow). The track vector (unbroken line) is drawn from the tail of the wind vector. In the model, we have a fixed (left) heading or (right) track in $10°$ intervals for $\pm 50°$ around the mean flight vector towards $180°$ (due south).



However, in the case of complete compensation, where the insects can only achieve certain directions under some wind conditions, some trigonometric calculations are not possible. Furthermore, an inconsistency arises when averaging track and heading because the numbers of available calculations in each wind condition are different. When $\alpha = 1.5$, an insect can achieve constant track towards $180°$ in nine of the wind conditions, while for the ratio $\alpha = 1.8$, $\alpha = 1.3$ and $\alpha = 1$, complete compensation can be achieved under 7, 11 and 17 wind conditions, respectively. When the angle between track direction and wind $\beta > 180° - \arcsin(1/\alpha)$ (e.g., $\beta = 140°$ when $\alpha = 1.5$), results are obtained but they have no physical meaning as they correspond to an insect's track being opposite to the desired direction.

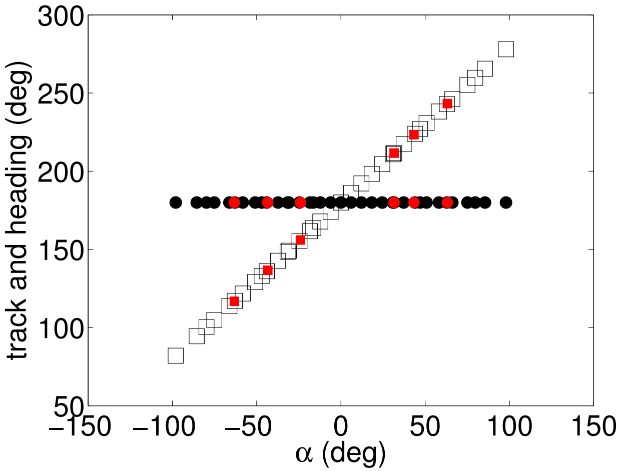
3 Results

Figure 5 demonstrates the regression method for the full drift and complete compensation models. It shows the relationships between the tracks and α averaged for each wind direction, or averaged over each wind sector, and the mean headings and mean α when $a = 1.5$.

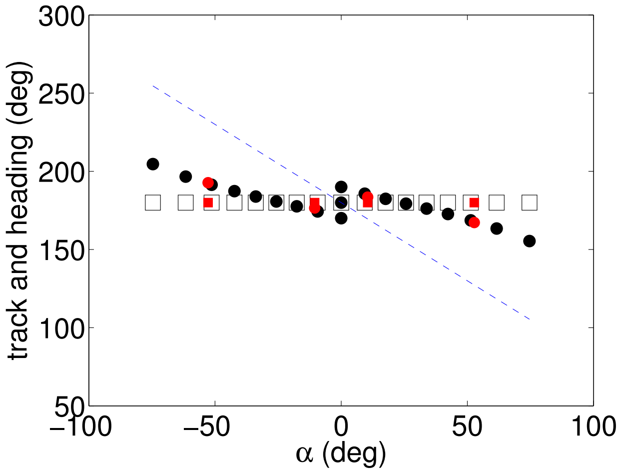
The analysis gives correct results with $b_{\text{track}} = 1$ and $b_{\text{head}} = 0$ in the full wind drift case (Figure 5(a)). When $a = 1.8$, $a = 1.3$ and $a = 1$, similar results are obtained. For the different a, only the range of the angle α varies. In the complete compensation case, when $a \leqslant 1$, Green and Alerstam [5] found $b_{\text{track}} = 0$ and $b_{\text{head}} = -1$ (the blue dashed line in Figure 5(b)); while in our case (points on Figure 5(b)) the expected linear results are not obtained. Similar results are obtained with $a = 1.3$ and $a = 1.5$, which suggest that the regression method is not able to demonstrate the full compensation case with a range of track directions for $a > 1$. The six-sector averaging approach leads to the same conclusion (Figure 5).

To illustrate the comparison method, Figure 6 shows the distribution of track and heading directions in winds from the left and right sides in relation to the average track direction for the cases of full wind drift (Figure 6(left)) and complete compensation (Figure 6(right)) from the model data. In the case of full drift, the results show that the mean track directions in left winds and right winds are significantly different (Watson–Williams test, $P = 0$), while the mean heading directions are the same ($P = 1$). We also calculate b_{track} and b_{head} by comparing the averaged track and heading in the winds coming from the left and the right sides of the mean track using equations (3) and (4). The calculations give the same results with $b_{\text{track}} = 1$ and $b_{\text{head}} = 0$ in the full wind drift case with all values of a. In the complete compensation case (Figure 6(b)), the results demonstrate that the mean track directions in left and right side winds are the same ($P = 1$); however, the mean heading directions in the left and right side winds are not significantly different ($P = 0.84$). This suggests that the comparison method is not always able to

Figure 5: The relationships between the average tracks (squares) and α, and the average headings (dots) and α. The ratio $a = 1.5$ and the different wind conditions are (a) full wind drift, and (b) complete compensation. We define each wind situation as winds from a $10°$ sector. The red symbols show the average value in the six sectors defined in Section 2.3. The blue dashed line in (b) shows the mean headings in relation to α when the ratio $a < 1.0$.

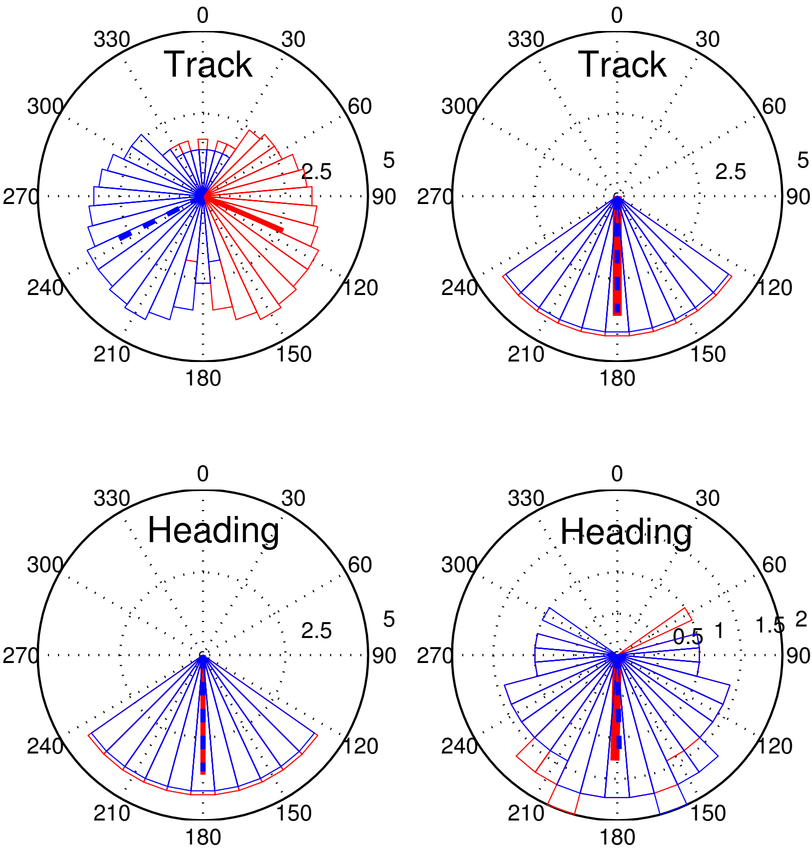


(a)



(b)

Figure 6: Distributions of (top) tracks and (bottom) headings for insects flying with (left) full wind drift and (right) full compensation when $a = 1.5$. The bottom-left heading plot and the top-right track plot show the assumed distributions of these quantities, and winds from the left and right are indistinguishable. The top-left track plot and the bottom-right heading plot show the variable quantities. Sectors show the percentage distribution in 10° intervals. Bars show the mean directions. Blue sectors show the insects flying in winds from the left, and red sectors show the insects flying in winds from the right.



demonstrate the full compensation case. With the other three α values, the results are mixed ($P = 0.19$ when $\alpha = 1.8$, $P = 0.06$ when $\alpha = 1.3$, $P = 0$ when $\alpha = 1.0$). This suggests that when $\alpha > 1.0$ the comparison method is not reliable as the restricted range of the angle between the track and wind β, means that the average heading can be spurious.

The results for both methods suggest that it is reasonable to use either the regression or comparison method to determine whether insects drift with the wind. However, they also demonstrated that it is not sensible to use either method to estimate whether insects compensate for the wind.

4 Conclusion

The regression method is a linear regression analysis of the mean track and heading directions in different winds relative to α and provides a direct means of measuring the magnitude of drift and its confidence interval. The comparison method compares the tracks and headings in the winds from the left and the right sides, and is superior for visualising the characteristics of the dataset. For the full drift case, these methods can be confidently used to evaluate the magnitude of drift as they both produce robust and reliable results. However, for the case of complete compensation, neither method was reliable for our model data as the migrating insects can only achieve complete compensations over a limited range of wind directions and averaging over this limited range can then give a spurious average heading. Even for $\alpha < 1$, Green and Alerstam [5] found their model gave spurious results when the range of wind directions in their model was restricted. In our case, for $\alpha > 1$, the restriction on the range of wind directions arises from the limited range of angles over which full compensation can be achieved, so similar spurious results are obtained. In future work we will investigate whether incorporating a range of α values in our model removes the limitation on the use of the comparison method in the full compensation case.

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