
http://dx.doi.org/10.1098/rsif.2018.0578
Social eavesdropping allows for a more risky gliding strategy by thermal-soaring birds

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Summary

Vultures are thought to form networks in the sky, with individuals monitoring the movements of others to gain up-to-date information on resource availability. While it is recognised that social information facilitates the search for carrion, how this facilitates the search for updrafts, another critical resource, remains unknown. In theory, birds could use information on updraft availability to modulate their flight speed, increasing their airspeed when informed on updraft location. In addition, the stylised circling behaviour associated with thermal soaring is likely to provide social cues on updraft availability for any bird operating in the surrounding area. We equipped five Gyps vultures with GPS and airspeed loggers to quantify the movements of birds flying in the same airspace. Birds that were socially informed on updraft availability immediately adopted higher airspeeds on entering the inter-thermal glide; a strategy that would be risky if birds were relying on personal information alone. This was embedded within a broader pattern of a reduction in airspeed (~3 m/s) through the glide, likely reflecting the need for low speed to sense and turn into the next thermal. Overall, this demonstrates, (i) the complexity of factors affecting speed selection over fine temporal scales, and (ii) that Gyps vultures respond to social information on the occurrence of energy in the aerial environment, which may reduce uncertainty in their movement decisions.

Keywords: Flight, social information, movement ecology, aeroecology, airspeed, risk
Introduction

Individuals require up-to-date information about their environment to optimise their movement strategies (1–3). Such information is particularly valuable for flying animals, as, not only is the aerial environment highly dynamic (4), but the nature of the air that animals experience can profoundly influence their flight costs. For instance, the metabolic costs of flapping flight by large birds can be up to 30 times resting metabolic rate (RMR), whereas soaring flight is around 2 x RMR (e.g. (5)). Large birds are therefore subject to strong selective pressure to locate and exploit updrafts as a means of subsidising their flight costs.

Nonetheless, birds have incomplete personal information on the availability of rising air, as the distribution of thermal updrafts, for instance, is chaotic in space and time and there is no evidence that birds are able to see or otherwise sense these updrafts remotely (though we know that human pilots and UAV’s can use cues from clouds and landscape features (6)). It has long been assumed that vultures would use social information to reduce the uncertainty associated with encountering ephemeral updrafts, by moving towards areas where other birds are gaining height in thermals (7). Crucially, such information would allow individuals to locate thermal updrafts and increase the speed that they glide between them (8–10), thereby increasing the likelihood that they will reach the updraft while it is profitable. However, high flight speeds are risky in the absence of information, as the height lost per unit time increases with airspeed (Figure 1). Thus, birds run the risk of reaching the ground before encountering the next area where air is rising. In fact it has been proposed that the risks associated with the rapid elevation loss, and the potential need to switch to flapping flight, explain why many birds glide more slowly than predicted by aeronautical models (11).

Testing the extent to which social information influences the route and behaviour of individuals as they glide between updrafts has been extremely difficult, due to the difficulty of (i) tracking multiple individuals simultaneously in real-world settings (though see recent work by Flack et al. (12)), and (ii) controlling or quantifying the social information available to birds during flight. Here, we test the hypothesis that birds should vary their airspeed in response to the availability of social information, using high-frequency GPS and airspeed sensors to track the flight behaviour of members of a group of vultures moving in the same airspace.

Methods

Data were collected from five Gyps vultures (Gyps himalayensis, n = 2, Gyps fulvus, n = 3) released to fly freely from the Rocher des Aigles falconry centre, Rocamadour, France.
Vultures were released in two groups split by age (3 adults and 2 immatures, Table 1), and staggered by 5 minutes, so that the first group (without initial information) could potentially provide social information for the second. The first group to be released alternated between releases. This protocol was carried out for 9 group flights, i.e. 3 flights on 3 consecutive days in the French summer when thermal updrafts were strong.

Prior to the first flight of each day, animal-attached GPS (Gipsy 1, TechnoSmart) and Daily Diary (DD) bio-logging units (produced by Swansea’s Laboratory for Animal Movement, cf. (13)) were attached to an aluminium plate, positioned on the lower back using a Teflon leg-loop harness (14). DD devices recorded acceleration and magnetic field strength (each in 3 axes), as well as temperature, barometric pressure and airspeed (through a forward facing Pitot tube attached to a differential pressure sensor, see below), at 40 Hz. Altitude (± 0.74 m) was calculated from the DD barometric pressure data (Pa, accurate to 1 Pa or 0.01 mbar), smoothed over 2 seconds, assuming standard atmospheric conditions and converted to metres given hourly sea-level pressure (taken from a local MétéoFrance weather station 20 km from the centre, accurate to 1hPa or 1 mbar). As the GPS unit took fixes at 4 Hz, all data were analysed at 4 Hz and duplicate timestamps in the GPS data were removed. This experimental setup allowed us to monitor i) the movements of all individuals soaring in the local area and ii) the thermal updrafts that a bird could choose to glide towards if it was using social information (see SM1 video).

Inter-thermal glides (glides) were identified as relatively straight periods of gliding between two thermal soaring events. The start and end of a glide was taken as the point at which birds either stopped or started circling within the thermal updraft, respectively, as identified using the magnetometry data (cf. (14), SM2). As birds are predicted to reduce airspeed during turning (8), glides were filtered to ensure that they were relatively straight and that they also corresponded to periods of sustained altitude loss. Accordingly, a total of 35 glides (of a possible 90) were taken forward for analyses (see also Table 1). These glides had a mean tortuosity (the straight-line distance/ total distance) of 0.84 ± 0.16 (SD; range 0.59) compared to 0.56 ± 0.34 (SD; range 0.97) for the glides that were removed. This also ensured that glides were not taken forward where the bird made decisions en-route that caused a change in direction. The length of the selected glides ranged from 45 ± 9 s (mean ± SD) to 98 ± 42 s, for each bird.

Airspeed calibration

A differential pressure sensor measured airflow (Volts) as the difference between static and dynamic pressure, with the latter recorded through a forward-facing brass Pitot tube (diameter
2 mm) that protruded from the DD housing (see (15,16) for methods of deriving airspeed with other data types). Airflow was converted to metres per second using a glide-specific wind vector \( V_w \), taken directly from the previous thermal as the rate at which an individual drifted while turning and gaining altitude in the thermal updraft (17). This ensured that the estimated wind vector was as good a representation as possible for each individual glide (noting also that the average altitude gained in a thermal was 52 m and altitude lost in a glide was 49 m). The wind vector in the previous thermal was used to calculate the birds’ airspeed \( V_a \) during 5 second periods of straight line flight (defined as zero tortuosity) in the subsequent glide \( n = 294 \), according to:

\[
V_a^2 = V_g^2 + V_w^2 + 2V_gV_w\cos\gamma
\]

Equation 1

where \( V_g \) is the mean ground speed vector for the 5 seconds, and \( \gamma \) is the angle between ground- and wind-speed vectors. We performed linear regressions to predict the airspeed \( \text{m/s} \) from the Pitot tube output (volts) for these straight glide periods (Table 1) and used the regression output to convert volts to m/s for each data point along the entire glide.

### Social information in inter-thermal glides

Each glide was divided into continuous 3-second steps (following (18)) and labelled according to the proportion of time through the glide (glide step). Within group flights \( N=9 \), each of the glides made by the 5 individuals \( N=35 \) were defined as either socially-informed or un-informed as follows. Glide-type was defined as informed when birds were informed about the presence of rising air by another bird, which had been soaring within a given radius of the focal bird’s entry point into that thermal, prior to, or within, the first 2 time steps of the glide (Figure 2). This 2-dimensional radius was taken as 2.5 times the average turning radius. We found that this radius allowed us to identify the shared use of a thermal updraft at a specific location. Increasing the threshold from 2 to 2.5 times the average turning radius increased the number of informed glides by 7, whereas a further increase from 2.5 to 3 times the average radius increased this number by only 1. This spatial overlap could have occurred prior to the start of the glide (but within the same group flight) or as the glide commenced (within the first two glide steps). Glides were defined as uninformed when there was no such spatial overlap in thermal soaring and birds glided to an updraft that had not been previously occupied by another individual during that group flight. Note that birds from both of the release groups undertook informed and uninformed glides, such that the determination of glide type depended on the circumstances of each individual glide, not the release order.
Analysis

A Welch Two Sample t-test was performed to quantify the difference in airspeed on entering the glide (glide step <0.05) between the two glide types, this being the point at which we established the availability of social information on the location of the next thermal. A generalized additive mixed-effects model (GAMM) was used to test the effect of the availability of social information on the airspeed of the focal bird in terms of how the pattern of change in airspeed through the glide differed between information contexts. We used thin plate regression splines and the by variable to include an interaction between the glide-type and a smoothed function of the glide step, with the number of bases per smooth term (k) set at a conservative value of 9 (mgcv R-software package (19,20)). The headwind component, previous climb rate and starting altitude were included as continuous linear terms. The headwind component ($V_h$) was calculated according to:

$$V_h = V_w \cos \theta$$  \hspace{1cm} \text{Equation 2}$$

where $V_w$ is the wind vector and $\theta$ the acute angle between the wind and the bird’s airspeed vector. Starting altitude was taken on entry into the glide. The previous climb rate was taken as the mean climb rate (m/s) achieved in the thermal soaring period immediately prior to the glide. We fitted random effects to control for potential non-independence of the glide, group-flight number and bird identity. The group-flight number was a three level factor that corresponded to each of the three group releases made on a single day, and was included to account for any increase in knowledge acquired relating to the thermal conditions for that day. Non-significant terms were dropped from the model via model simplification, comparing GAMMs with and without the term of interest via an anova function (all analyses were performed in R version 3.3.1).

Results

At the point when birds began their inter-thermal glides (glide step ≤ 0.05), those with social information on the location of the next thermal had significantly higher airspeeds (17.0 m/s) compared to those without (15.8 m/s) ($t = -2.25$, df= 15.46, $p = 0.034$). Absolute airspeed was also higher for glides starting at greater altitudes (est. = 0.0037, $t = 4.31$, p<0.001) but there was no significant difference in starting altitude between informed and uninformed glides ($t = -0.149$, df= 15.5, $p = 0.884$, informed mean starting altitude was 480.6 m and uninformed = 492.0 m). Following this decision point, all birds were predicted to reduce their airspeed through the glide to ~12 m/s at the end of the glide (informed= 12.7 ± 0.4 m/s, uninformed = 12.1 ± 0.4 m/s,) (Figure 3). The form of the pattern of change through the glide differed
fundamentally according to the availability of social information (Table 2), with informed
glides showing a consistent decrease in airspeed through time (EDF = 1.906, p<0.001) and
uninformed glides showing more of a hump-shaped pattern in airspeed through the glide
(EDF = 5.906, p<0.001). The final candidate model did not include flight number as a random
factor, though bird ID and glide did explain a significant amount of variance in airspeed and
were retained in the model.

Discussion

The role of social information in shaping the movement decisions of birds in flight has long
been assumed (7,21,22). Here, we show that birds do indeed vary their glide speed in
response to the presence of social information (Table 2, Figure 3), and in a manner that aligns
with aeronautical predictions (cf. (9)). At the start of the glide, birds with access to social
information adopted higher airspeeds (17.0 m/s) compared to those relying on personal
information (15.8 m/s). The only point at which it is possible to assess the influence of social
information on airspeed selection is at the start of the glide, where they were categorised as
‘informed’, or ‘uninformed’. The context may change beyond this point with uninformed
birds becoming informed en route (if other individuals arrive at this second thermal after a
bird enters its inter-thermal glide). Interestingly, the fact that the informed birds opted for fast
speeds at the start of the glide meant that they would have moved through the region of
sinking air surrounding the thermal core relatively quickly. The increase in speed part way
through the glide by uninformed birds (the peak speed at 25% though the glide, Figure 3)
likely represents a response to this downdraft, with bird increasing speed to move through this
region quickly.

Birds are known to vary their airspeed between climb-glide cycles, e.g. in relation to the
previous climb rate (11), the headwind component (18,23) and whether or not the destination
is familiar (24). Furthermore, previous work has shown that captive birds still fly in an
efficient manner in line with aeronautical predictions (e.g. (18,25)). However, the framework
that has been developed to predict optimal glide speeds, as well as previous experimental
work to test whether airspeeds conform to these predictions, has assumed that birds select a
single speed within the glide (7,10) (cf. (18)). Our results show that birds reduce their
airspeed through the glide (here to ~12 m/s, Figure 3). This reduction in speed is likely to be
important for a bird’s ability to (i) detect and (ii) turn into, the next thermal updraft;
constraints that are equally pertinent with or without social information.
The difference between the fastest and slowest predicted speeds within glides was substantial in these vultures (~3 m/s). In fact it is almost as great as the difference between the two theoretical optima that are the foundations for all predictions regarding airspeed selection i.e. the minimum sink speed, $V_{ms}$ (the speed at which the bird loses height at the minimum rate) and the best glide speed, $V_{bg}$ (the speed at which birds maximise distance gained per unit of altitude lost) (here that difference is ~4.5 m/s) (8,26,27). Our results therefore point to hitherto unquantified complexity in speed selection within individual glides (cf. (26)). This reflects the fact that both physical and biological environments can change within a glide. At much greater altitudes of up to 6000 m, Sherub et al. (15) found that birds increase their airspeed (in thermal soaring) in relation to the decreasing air densities. Though the elevation range is much lower in this study, our results suggest that birds soaring up to these heights may experience even greater changes in airspeed through the glide. As the environment changes through the glide, so too will the currency that birds will prioritise, be it maximising the distance flown or minimising the risks associated with locating the next thermal updraft. It is likely that these latter risks also explain why birds leaving a thermal with more altitude adopt higher, and potentially riskier, flight speeds (Table 2: estimate = 0.0037, t = 4.31, p<0.001) (also see (11)).

Human pilots are often reported to use soaring birds to locate their next updraft (25), so we might expect vultures to behave in a similar manner. Indeed, vultures are known to respond to rapid descents of other birds as a cue for the location of a carcass (21,28,29). Thermal soaring is a similarly stylized behaviour, with vultures banking to maintain position within an updraft. For birds with relatively high visual acuity (30), such movements could provide a cue not only for updraft availability, but also the profitability of the updraft, with the bird’s climb rate indicating the strength of the updraft (cf. (31)), analogous to public information on patch quality in foraging (32). Interestingly, we found some suggestion that vultures glided towards birds experiencing the greatest climb rate when individuals were informed about the location of multiple updrafts (the median vertical velocity achieved by the followed bird was 0.6 ± 0.5 m/s compared to 0.4 ± 0.7 m/s for birds in other thermals at the same time). However, the preference for strong thermals cannot be tested for here as the number of options available at any one decision-point was limited by the number of birds in the study.

Both carcasses and thermal updrafts are ephemeral resources, with the potential to “decay” over timescales of minutes (33). There should therefore be strong selective pressure for individuals to exploit social cues that provide information on the availability of both (cf. (28)). Our results support the idea that social information could facilitate flight performance in an analogous fashion to the use of social facilitation in the search for carcasses, with
individuals being able to increase their cross-country speed when operating within the range of other soaring birds (cf. (9)). By sensing the environment through the movement of others, birds could make decisions that can increase the efficiency of their own movement through the same space (Figure 1). This can manifest at different scales of movement depending on proximity to others and the scale of environmental variation. Nagy et al. (34), for example, report the effects of social interactions over very fine timescales, demonstrating that storks soaring within the same thermal updraft can pool the experience of each individual to map the distribution of uplift in the thermal via collective sensing. Our results support the idea that groups of soaring birds can eavesdrop on the movements of individuals that occupy a more distant position in time and space. Such up-to-date information could be considered alongside their own knowledge of the environment, to increase movement performance above what could be achieved with personal information alone. This leads to the question of whether there is an optimal distance over which social eavesdropping would provide the most accurate information given spatial-temporal variation in flying conditions. For information to be valuable in soaring-gliding flight, the distance between birds would have to be great enough to assist the focal bird in covering ground, but not be so great that the next thermal has ceased to rise or shift substantially in location.

Overall, we show that soaring birds can respond to social cues that provide up-to-date information on thermal availability. Such processes could have implications for route choice (35) and wider patterns of space-use in vultures and in other birds. This is likely to hold true whether or not animals are using soaring flight, as eavesdropping could provide information about the distribution of air currents that impact flight control (e.g. (36)) as well as rates of energy use. We therefore see great opportunities for further research uniting the aeronautical and social information paradigms.

Acknowledgments
We thank D. Maylin and R. Arnaud at Rocher des Aigles as well as all of their staff for their patience and enthusiasm for the project. We also thank S. Potier and J. Fluhr for their help with tag deployments. GPS loggers were provided by Giacomo Dell’Omo. DD housings were designed by P. Hopkins and hardware by M. Holton at Swansea University. The authors declare no competing interests

Funding statement
HW was supported by a Swansea University Studentship.
The permit for equipping vultures with loggers was provided as part of the licence of O. Duriez from the Research Centre for Bird Population Studies (CRBPO) of the Natural History Museum (MNHN, Paris). Birds were handled by their usual trainer, under the permit of the Rocher des Aigles.

**Author Contributions**

The study was conceived and the article drafted by HJW, ELCS and AJK. Data were collected by HW and OD, and analysed by HW with input from all authors. All authors critically revised the manuscript.

**Data Availability**

All data collected from the onboard devices have been uploaded to a Movebank data repository and can be accessed using DOI 10.5441/001/1.4f03k6s5.

**References**

30. Fischer AB. Laboratory experiments on, and open-country observations of the visual acuity and behaviour, of old world vultures. University of Muenster, Germany; 1969.


Table 1: Biometrics and gliding airspeeds for individual vultures. Birds showed inter-individual differences in airspeeds ($V_a$) through the glide ($F = 214.1_{10410}$, $p<0.001$) and their median airspeeds were greater than their $V_{bg}$, calculated from the following biometric data; wing loading (in kg.m$^{-2}$) (WL), aspect ratio (AR) and mass (kg) (M). The theoretical minimum sink ($V_{ms}$) and best glide speeds ($V_{bg}$) are given for reference, as are the numbers of inter-thermal glides (ITGs) performed by the bird that were defined as non-social (S1) and social (S2).

<table>
<thead>
<tr>
<th>Vulture (age)</th>
<th>Biometrics</th>
<th>ITG (s)</th>
<th>Theoretical optima</th>
<th>$V_a$ (m/s)</th>
<th>$V_a$ Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>G. fulvus</strong></td>
<td>WL: 7.77</td>
<td>44.8 ± 9.2</td>
<td>$V_{bg}$: 14.4 m/s</td>
<td>14.86 ± 1.49</td>
<td>$V_a = 0.0022P_{volts} - 5.33$</td>
</tr>
<tr>
<td>Adult (18)</td>
<td>AR: 6.61</td>
<td>(N = 4)</td>
<td>$V_{ms}$: 9.20 m/s</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M: 7.7</td>
<td>S1 = 4, S2= 0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>G. fulvus</strong></td>
<td>WL: 7.28</td>
<td>98.0 ± 42.0</td>
<td>$V_{bg}$: 13.8 m/s</td>
<td>16.30 ± 2.58</td>
<td>$V_a = 0.0063P_{volts} - 41.56$</td>
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<tr>
<td>Immature (3)</td>
<td>AR: 6.88</td>
<td>(N = 8)</td>
<td>$V_{ms}$: 8.80 m/s</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M: 7.14</td>
<td>S1 = 4, S2= 3</td>
<td></td>
<td></td>
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<tr>
<td><strong>G. fulvus</strong></td>
<td>WL: 7.06</td>
<td>67.1 ± 50.6</td>
<td>$V_{bg}$: 13.7 m/s</td>
<td>15.11 ± 2.57</td>
<td>$V_a = 0.0056P_{volts} - 36.65$</td>
</tr>
<tr>
<td>Immature (4)</td>
<td>AR: 6.73</td>
<td>(N = 6)</td>
<td>$V_{ms}$: 8.70 m/s</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>M: 7.2</td>
<td>S1 = 5, S2= 1</td>
<td></td>
<td></td>
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<tr>
<td><strong>G. himalayensis</strong></td>
<td>WL: 7.18</td>
<td>77.0 ± 50.8</td>
<td>$V_{bg}$: 13.8 m/s</td>
<td>16.34 ± 2.80</td>
<td>$V_a = 0.0045P_{volts} - 26.42$</td>
</tr>
<tr>
<td>Adult (19)</td>
<td>AR: 6.95</td>
<td>(N = 10)</td>
<td>$V_{ms}$: 8.70 m/s</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>M: 8.1</td>
<td>S1 = 6, S2= 4</td>
<td></td>
<td></td>
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<tr>
<td><strong>G. himalayensis</strong></td>
<td>WL: 6.63</td>
<td>62.7 ± 38.6</td>
<td>$V_{bg}$: 13.8 m/s</td>
<td>16.56 ± 3.47</td>
<td>$V_a = 0.0047P_{volts} - 28.33$</td>
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<td>Immature (4)</td>
<td>AR: 5.98</td>
<td>(N = 8)</td>
<td>$V_{ms}$: 8.70 m/s</td>
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<td>M: 8.45</td>
<td>S1 = 5, S2= 3</td>
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</table>
Table 2: Factors affecting speed selection during inter-thermal glides. The GAMM output predicts the effect of the starting altitude (lme) and the time through the glide (glide step) (as an additive effect) in interaction with glide type (informed or uninformed) (n = 857) on airspeed. There is a significant pattern of change in airspeed through the glide for both glide types, although this was more complex for uninformed glides than it was for informed glides; as indicated by the estimated degrees of freedom (EDF). Airspeed in the glide was also greater for glides starting at a high altitude.

<table>
<thead>
<tr>
<th>lme</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t-value</th>
<th>p-value</th>
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<td>(Intercept)</td>
<td>14.08</td>
<td>0.482</td>
<td>29.20</td>
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<td>Starting altitude</td>
<td>0.004</td>
<td>0.0008</td>
<td>4.31</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>gam</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glide step : uninformed</td>
<td>5.906</td>
<td>60.08</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Glide step : informed</td>
<td>1.906</td>
<td>34.15</td>
<td>&lt;0.0001</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1. The potential value of social information in aiding route selection in a dynamic environment. Each horizontal line represents a moment in time along a trajectory in 2-dimensional space. The variation about the horizontal for each line represents the vertical velocity of the air; so that a deviation below and above the horizontal represents a downdraft and an updraft respectively (the intensity represented in the amplitude of deviation). A bird (black) moving through space must also move through time so that a soaring bird gliding between thermals could follow a track such as that shown by the solid grey line. Here it adopts a slow airspeed within the first thermal and at some point (in this case when the thermal decreases in intensity) decides to glide to the next thermal. As it glides, it increases the distance gained per unit time and then slows as it reaches the next updraft. The presence of another bird i.e. the producer (grey), soaring in the second updraft could provide information that allows the focal bird to increase the efficiency of the route taken (dashed grey line), in terms of (i) the point at which the receiver decides to leave its current updraft, (ii) the increased airspeed adopted in the glide and (iii) the reduction in time and altitude required to locate the strongest part of the next thermal.
Figure 2: The 2-dimensional track of a socially-informed glide (red) between two thermal soaring periods (black). The start of the glide is highlighted (orange cross), along with the radius (blue circle) used to identify spatial overlap in soaring behaviour. The soaring of a second vulture (purple trajectory) within this radius, prior to the focal bird entering the glide, defined this case as a socially-informed glide. The glide trajectory is from right to left as the focal vulture moved between thermals.
Figure 3: Airspeed varied with time through the glide and access to social information. The pattern of decreasing airspeed through the glide was predicted by the smoothed component of the GAMM in interaction with glide type. The form of this general decrease differed between a) non-social (EDF = 5.91, F = 60.08, p < 0.001, n = 599) and b) social glides (EDF = 1.91, F = 34.15, p < 0.001, n = 258). The best glide ($V_{bg}$) and minimum sink ($V_{ms}$) speeds for these birds are given for reference.