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1 **Social eavesdropping allows for a more risky gliding strategy by thermal-soaring birds**

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11
12 **Summary**

13
14 Vultures are thought to form networks in the sky, with individuals monitoring the movements
15 of others to gain up-to-date information on resource availability. While it is recognised that
16 social information facilitates the search for carrion, how this facilitates the search for updrafts,
17 another critical resource, remains unknown. In theory, birds could use information on updraft
18 availability to modulate their flight speed, increasing their airspeed when informed on updraft
19 location. In addition, the stylised circling behaviour associated with thermal soaring is likely to
20 provide social cues on updraft availability for any bird operating in the surrounding area. We
21 equipped five *Gyps* vultures with GPS and airspeed loggers to quantify the movements of birds
22 flying in the same airspace. Birds that were socially informed on updraft availability
23 immediately adopted higher airspeeds on entering the inter-thermal glide; a strategy that would
24 be risky if birds were relying on personal information alone. This was embedded within a
25 broader pattern of a reduction in airspeed (~3 m/s) through the glide, likely reflecting the need
26 for low speed to sense and turn into the next thermal. Overall, this demonstrates, (i) the
27 complexity of factors affecting speed selection over fine temporal scales, and (ii) that *Gyps*
28 vultures respond to social information on the occurrence of energy in the aerial environment,
29 which may reduce uncertainty in their movement decisions.

30
31 **Keywords:** Flight, social information, movement ecology, aeroecology, airspeed, risk

32

33 **Introduction**

34 Individuals require up-to-date information about their environment to optimise their movement
35 strategies (1–3). Such information is particularly valuable for flying animals, as, not only is the
36 aerial environment highly dynamic (4), but the nature of the air that animals experience can
37 profoundly influence their flight costs. For instance, the metabolic costs of flapping flight by
38 large birds can be up to 30 times resting metabolic rate (RMR), whereas soaring flight is around
39 2 x RMR (e.g. (5)). Large birds are therefore subject to strong selective pressure to locate and
40 exploit updrafts as a means of subsidising their flight costs.

41

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

56

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

64

65 **Methods**

66

67 Data were collected from five *Gyps* vultures (*Gyps himalayensis*, n = 2, *Gyps fulvus*, n = 3)
68 released to fly freely from the Rocher des Aigles falconry centre, Rocamadour, France.
69 Vultures were released in two groups split by age (3 adults and 2 immatures, Table 1), and

70 staggered by 5 minutes, so that the first group (without initial information) could potentially
71 provide social information for the second. The first group to be released alternated between
72 releases. This protocol was carried out for 9 group flights, i.e. 3 flights on 3 consecutive days
73 in the French summer when thermal updrafts were strong.

74
75 Prior to the first flight of each day, animal-attached GPS (Gipsy 1, TechnoSmart) and Daily
76 Diary (DD) bio-logging units (produced by Swansea's Laboratory for Animal Movement, *cf.*
77 (13)) were attached to an aluminium plate, positioned on the lower back using a Teflon leg-
78 loop harness (14). DD devices recorded acceleration and magnetic field strength (each in 3
79 axes), as well as temperature, barometric pressure and airspeed (through a forward facing Pitot
80 tube attached to a differential pressure sensor, see below), at 40 Hz. Altitude (± 0.74 m) was
81 calculated from the DD barometric pressure data (Pa, accurate to 1 Pa or 0.01 mbar), smoothed
82 over 2 seconds, assuming standard atmospheric conditions and converted to metres given
83 hourly sea-level pressure (taken from a local MétéoFrance weather station 20 km from the
84 centre, accurate to 1hPa or 1 mbar). As the GPS unit took fixes at 4 Hz, all data were analysed
85 at 4 Hz and duplicate timestamps in the GPS data were removed. This experimental setup
86 allowed us to monitor i) the movements of all individuals soaring in the local area and ii) the
87 thermal updrafts that a bird could choose to glide towards if it was using social information
88 (see SM1 video).

89
90 Inter-thermal glides (*glides*) were identified as relatively straight periods of gliding between
91 two thermal soaring events. The start and end of a glide was taken as the point at which birds
92 either stopped or started circling within the thermal updraft, respectively, as identified using
93 the magnetometry data (*cf.* (14), SM2). As birds are predicted to reduce airspeed during turning
94 (8), glides were filtered to ensure that they were relatively straight and that they also
95 corresponded to periods of sustained altitude loss. Accordingly, a total of 35 glides (of a
96 possible 90) were taken forward for analyses (see also Table 1). These glides had a mean
97 tortuosity (the straight-line distance/ total distance) of 0.84 ± 0.16 (SD; range 0.59) compared
98 to 0.56 ± 0.34 (SD; range 0.97) for the glides that were removed. This also ensured that glides
99 were not taken forward where the bird made decisions *en-route* that caused a change in
100 direction. The length of the selected glides ranged from 45 ± 9 s (mean \pm SD) to 98 ± 42 s, for
101 each bird.

102

103 *Airspeed calibration*

104 A differential pressure sensor measured airflow (Volts) as the difference between static and
105 dynamic pressure, with the latter recorded through a forward-facing brass Pitot tube (diameter
106 2 mm) that protruded from the DD housing (see (15,16) for methods of deriving airspeed with

107 other data types). Airflow was converted to metres per second using a glide-specific wind
108 vector (V_w), taken directly from the previous thermal as the rate at which an individual drifted
109 while turning and gaining altitude in the thermal updraft (17). This ensured that the estimated
110 wind vector was as good a representation as possible for each individual glide (noting also that
111 the average altitude gained in a thermal was 52 m and altitude lost in a glide was 49 m). The
112 wind vector in the previous thermal was used to calculate the birds' airspeed (V_a) during 5
113 second periods of straight line flight (defined as zero tortuosity) in the subsequent glide (n =
114 294), according to:

115

$$116 \quad V_a^2 = V_g^2 + V_w^2 + 2V_g V_w \cos \gamma \quad \text{Equation 1}$$

117

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

122

123 *Social information in inter-thermal glides*

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

141

142 *Analysis*

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

154

$$155 \quad V_h = V_w \cos \theta \quad \text{Equation 2}$$

156

157 where V_w is the wind vector and θ the acute angle between the wind and the bird's airspeed
158 vector. Starting *altitude* was taken on entry into the glide. The previous *climb* rate was taken as
159 the mean climb rate (m/s) achieved in the thermal soaring period immediately prior to the glide.
160 We fitted random effects to control for potential non-independence of the glide, group-flight
161 number and bird identity. The group-flight number was a three level factor that corresponded
162 to each of the three group releases made on a single day, and was included to account for any
163 increase in knowledge acquired relating to the thermal conditions for that day. Non-significant
164 terms were dropped from the model via model simplification, comparing GAMMs with and
165 without the term of interest via an anova function (all analyses were performed in R version
166 3.3.1).

167

168 **Results**

169

170 At the point when birds began their inter-thermal glides (*glide step* ≤ 0.05), those with social
171 information on the location of the next thermal had significantly higher airspeeds (17.0 m/s)
172 compared to those without (15.8 m/s) ($t = -2.25$, $df = 15.46$, $p = 0.034$). Absolute airspeed was
173 also higher for glides starting at greater altitudes (est. = 0.0037, $t = 4.31$, $p < 0.001$) but there
174 was no significant difference in starting altitude between informed and uninformed glides ($t =$
175 -0.149 , $df = 15.5$, $p = 0.884$, *informed* mean starting altitude was 480.6 m and *uninformed* 492.0
176 m). Following this decision point, all birds were predicted to reduce their airspeed through the
177 glide to ~ 12 m/s at the end of the glide (*informed* = 12.7 ± 0.4 m/s, *uninformed* = 12.1 ± 0.4
178 m/s,) (Figure 3). The form of the pattern of change through the glide differed fundamentally
179 according to the availability of social information (Table 2), with informed glides showing a

180 consistent decrease in airspeed through time (EDF = 1.906, $p < 0.001$) and uninformed glides
181 showing more of a hump-shaped pattern in airspeed through the glide (EDF = 5.906, $p < 0.001$).
182 The final candidate model did not include flight number as a random factor, though bird ID and
183 glide did explain a significant amount of variance in airspeed and were retained in the model.

184

185 **Discussion**

186

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

201

202 Birds are known to vary their airspeed between climb-glide cycles, e.g. in relation to the
203 previous climb rate (11), the headwind component (18,23) and whether or not the destination
204 is familiar (24). Furthermore, previous work has shown that captive birds still fly in an efficient
205 manner in line with aeronautical predictions (e.g. (18,25)). However, the framework that has
206 been developed to predict optimal glide speeds, as well as previous experimental work to test
207 whether airspeeds conform to these predictions, has assumed that birds select a single speed
208 within the glide (7,10) (cf. (18)). Our results show that birds reduce their airspeed through the
209 glide (here to ~12 m/s, Figure 3). This reduction in speed is likely to be important for a bird's
210 ability to (i) detect and (ii) turn into, the next thermal updraft; constraints that are equally
211 pertinent with or without social information.

212

213 The difference between the fastest and slowest predicted speeds within glides was substantial
214 in these vultures (~3 m/s). In fact it is almost as great as the difference between the two
215 theoretical optima that are the foundations for all predictions regarding airspeed selection i.e.
216 the minimum sink speed, V_{ms} (the speed at which the bird loses height at the minimum rate) and

217 the best glide speed, V_{bg} (the speed at which birds maximise distance gained per unit of altitude
218 lost)(here that difference is ~ 4.5 m/s) (8,26,27). Our results therefore point to hitherto
219 unquantified complexity in speed selection within individual glides (*cf.* (26)). This reflects the
220 fact that both physical and biological environments can change within a glide. At much greater
221 altitudes of up to 6000 m, Sherub *et al.* (15) found that birds increase their airspeed (in thermal
222 soaring) in relation to the decreasing air densities. Though the elevation range is much lower
223 in this study, our results suggest that birds soaring up to these heights may experience even
224 greater changes in airspeed through the glide. As the environment changes through the glide,
225 so too will the currency that birds will prioritise, be it maximising the distance flown or
226 minimising the risks associated with locating the next thermal updraft. It is likely that these
227 latter risks also explain why birds leaving a thermal with more altitude adopt higher, and
228 potentially riskier, flight speeds (Table 2: estimate = 0.0037, $t = 4.31$, $p < 0.001$) (also see (11)).
229

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

243
244 Both carcasses and thermal updrafts are ephemeral resources, with the potential to “decay” over
245 timescales of minutes (33). There should therefore be strong selective pressure for individuals
246 to exploit social cues that provide information on the availability of both (*cf.* (28)). Our results
247 support the idea that social information could facilitate flight performance in an analogous
248 fashion to the use of social facilitation in the search for carcasses, with individuals being able
249 to increase their cross-country speed when operating within the range of other soaring birds (*cf.*
250 (9)). By sensing the environment through the movement of others, birds could make decisions
251 that can increase the efficiency of their own movement through the same space (Figure 1). This
252 can manifest at different scales of movement depending on proximity to others and the scale of
253 environmental variation. Nagy *et al.* (34), for example, report the effects of social interactions

254 over very fine timescales, demonstrating that storks soaring within the same thermal updraft
255 can pool the experience of each individual to map the distribution of uplift in the thermal via
256 collective sensing. Our results support the idea that groups of soaring birds can eavesdrop on
257 the movements of individuals that occupy a more distant position in time and space. Such up-
258 to-date information could be considered alongside their own knowledge of the environment, to
259 increase movement performance above what could be achieved with personal information
260 alone. This leads to the question of whether there is an optimal distance over which social
261 eavesdropping would provide the most accurate information given spatial-temporal variation
262 in flying conditions. For information to be valuable in soaring-gliding flight, the distance
263 between birds would have to be great enough to assist the focal bird in covering ground, but
264 not be so great that the next thermal has ceased to rise or shift substantially in location.

265

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

273

274

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280 no competing interests

281

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284

285 **Ethics**

286 The permit for equipping vultures with loggers was provided as part of the licence of O. Duriez
287 from the Research Centre for Bird Population Studies (CRBPO) of the Natural History Museum
288 (MNHN, Paris). Birds were handled by their usual trainer, under the permit of the Rocher des
289 Aigles.

290

291 **Author Contributions**

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

295

296 **Data Availability**

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

299

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385 **Table 1: Biometrics and gliding airspeeds for individual vultures.** Birds showed inter-
 386 individual differences in airspeeds (V_a) through the glide ($F = 214.1_{10410, 4}$, $p < 0.001$) and their
 387 median airspeeds were greater than their V_{bg} , calculated from the following biometric data;
 388 wing loading (in $\text{kg}\cdot\text{m}^{-2}$) (WL), aspect ratio (AR) and mass (kg) (M). The theoretical minimum
 389 sink (V_{ms}) and best glide speeds (V_{bg}) are given for reference, as are the numbers of inter-thermal
 390 glides (ITGs) performed by the bird that were defined as non-social (S1) and social (S2).

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Vulture (age)	Biometrics	ITG (s)	Theoretical optima	V_a (m/s)	V_a Regression
<i>G. fulvus</i> Adult (18)	WL: 7.77 AR: 6.61 M: 7.7	44.8 ± 9.2 (N = 4) S1 = 4, S2 = 0	V_{bg} : 14.4 m/s V_{ms} : 9.20 m/s	14.86 ± 1.49	$V_a = 0.0022P_{volts} - 5.33$
<i>G. fulvus</i> Immature (3)	WL: 7.28 AR: 6.88 M: 7.14	98.0 ± 42.0 (N = 8) S1 = 4, S2 = 3	V_{bg} : 13.8 m/s V_{ms} : 8.80 m/s	16.30 ± 2.58	$V_a = 0.0063P_{volts} - 41.56$
<i>G. fulvus</i> Immature (4)	WL: 7.06 AR: 6.73 M: 7.2	67.1 ± 50.6 (N = 6) S1 = 5, S2 = 1	V_{bg} : 13.7 m/s V_{ms} : 8.70 m/s	15.11 ± 2.57	$V_a = 0.0056P_{volts} - 36.65$
<i>G. himalayensis</i> Adult (19)	WL: 7.18 AR: 6.95 M: 8.1	77.0 ± 50.8 (N = 10) S1 = 6, S2 = 4	V_{bg} : 13.8 m/s V_{ms} : 8.70 m/s	16.34 ± 2.80	$V_a = 0.0045P_{volts} - 26.42$
<i>G. himalayensis</i> Immature (4)	WL: 6.63 AR: 5.98 M: 8.45	62.7 ± 38.6 (N = 8) S1 = 5, S2 = 3	V_{bg} : 13.8 m/s V_{ms} : 8.70 m/s	16.56 ± 3.47	$V_a = 0.0047P_{volts} - 28.33$

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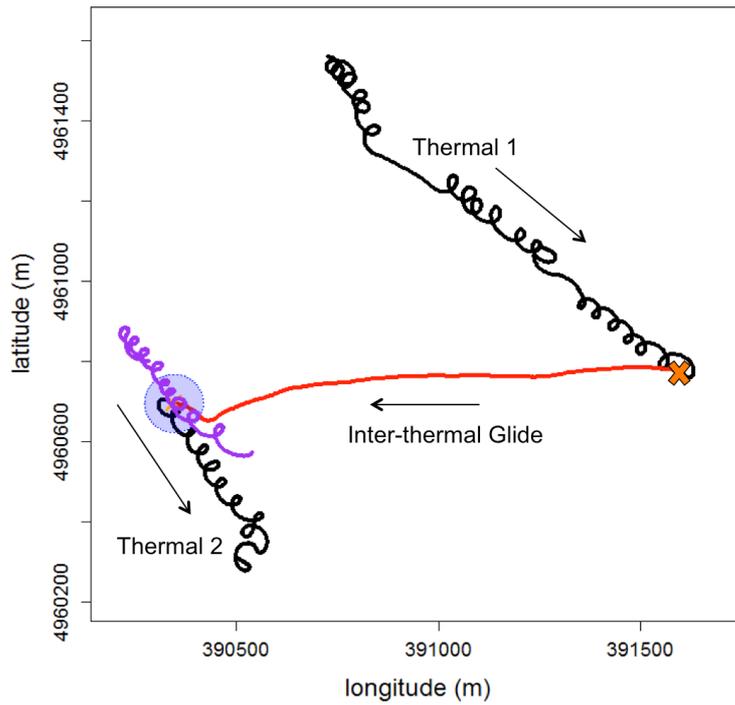
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395 **Table 2: Factors affecting speed selection during inter-thermal glides.** The GAMM output
 396 predicts the effect of the starting altitude (*lme*) and the time through the glide (*glide step*) (as
 397 an additive effect) in interaction with glide type (*informed* or *uninformed*) (n = 857) on airspeed.
 398 There is a significant pattern of change in airspeed through the glide for both glide types,
 399 although this was more complex for uninformed glides than it was for informed glides; as
 400 indicated by the estimated degrees of freedom (EDF). Airspeed in the glide was also greater for
 401 glides starting at a high altitude.

402

lme	Estimate	Std. Error	t-value	p-value
(Intercept)	14.08	0.482	29.20	<0.0001
Starting altitude	0.004	0.0008	4.31	<0.0001
gam	EDF	F-value	p-value	
Glide step : uninformed	5.906	60.08	<0.0001	
Glide step : informed	1.906	34.15	<0.0001	

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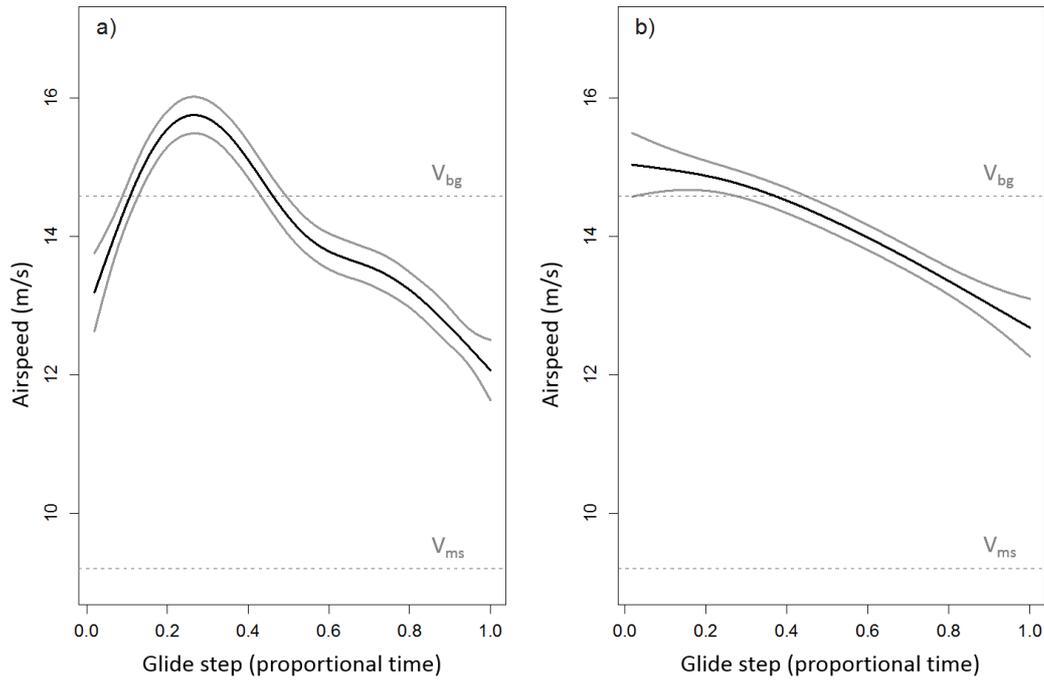


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423 **Figure 2: The 2-dimensional track of a socially-informed glide (red) between two thermal**
 424 **soaring periods (black).** The start of the glide is highlighted (orange cross), along with the
 425 radius (blue circle) used to identify spatial overlap in soaring behaviour. The soaring of a second
 426 vulture (purple trajectory) within this radius, prior to the focal bird entering the glide, defined
 427 this case as a socially-informed glide. The glide trajectory is from right to left as the focal
 428 vulture moved between thermals.

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431

432 **Figure 3: Airspeed varied with time through the glide and access to social information.**

433 The pattern of decreasing airspeed through the glide was predicted by the smoothed component
 434 of the GAMM in interaction with glide type. The form of this general decrease differed between
 435 a) non-social (EDF = 5.91, F = 60.08, $p < 0.001$, n = 599) and b) social glides (EDF = 1.91, F =
 436 34.15, $p < 0.001$, n = 258). The best glide (V_{bg}) and minimum sink (V_{ms}) speeds for these birds
 437 are given for reference.