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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

## 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

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 ($\pm$ 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 $\pm$ 0.16 (SD; range 0.59) compared

98   to 0.56 $\pm$ 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 $\pm$ 9 s (mean $\pm$ SD)  to 98 $\pm$ 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

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:

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

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 (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*

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                                    $$V_h = V_w \cos \theta$$                                    Equation 2

156

157    where $V_w$ is the wind vector and $\theta$ 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* $\leq 0.05$), 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 $0.6 \pm 0.5$ m/s

240  compared to $0.4 \pm 0.7$ 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

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.

**Ethics**

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.

**References**

1. Rafacz M, Templeton JJ. Environmental unpredictability and the value of social information for foraging starlings. Ethology. 2003;109:951–60.

2. Dechmann DKN, Heucke SL, Giuggioli L, Safi K, Voigt CC, Wikelski M. Experimental evidence for group hunting via eavesdropping in echolocating. Proc R Soc B. 2009;276(1668):2721–8.

3. Dall SRX, Giraldeau L, Olsson O, Mcnamara JM, Stephens DW. Information and its use by animals in evolutionary ecology. Trends Ecol Evol. 2005;20(4):187–93.

4. Shepard ELC, Ross AN, Portugal SJ. Moving in a moving medium: new perspectives on flight. Philos Trans R Soc B. 2016;371(1704).

5. Elliott KH, Ricklefs RE, Gaston AJ, Hatch SA, Speakman JR, Davoren GK. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. Proc Natl Acad Sci. 2013;110(23):9380–4.

6. Stolle M, Bolting J, Döll C, Watanabe Y. A vision-based Flight Guidance and Navigation System for autonomous cross-country soaring UAVs. 2015 Int Conf ce Unmanned Aircr Syst. 2015;June 9-12.

7. Pennycuick CJ. Soaring behaviour and performance of some East African birds observed from a motor-glider. Ibis (Lond 1859). 1972;114(178–218).

8. Pennycuick CJ. Modelling the Flying Bird. Vol. 5. 1st Editio. Boston: Elsevier; 2008.

9. van Loon EE, Shamoun-Baranes J, Bouten W, Davis SL. Understanding soaring bird migration through interactions and decisions at the individual level. J Theor Biol. 2011;270:112–26.

10. MacCready P. B. Optimum airspeed selector. Soaring. 1958;Jan-Feb:10–1.

11. Horvitz N, Sapir N, Liechti F, Avissar R, Mahrer I, Nathan R. The gliding speed of migrating birds: slow and safe or fast and risky? Ecol Lett. 2014;17(6):670–9.

12. Flack A, Nagy M, Fiedler W, Couzin ID, Wikelski M. From local collective behaivour to global migratory patterns in white storks. Science (80- ). 2018;360:911–4.

13. Wilson RP, Shepard ELC, Liebsch N. Prying into the intimate details of animal lives: Use of a daily diary on animals. Endanger Species Res. 2008;4(1–2):123–37.

14. Williams HJ, Shepard ELC, Duriez O, Lambertucci S a. Can accelerometry be used to distinguish between flight types in soaring birds? Anim Biotelemetry. BioMed Central; 2015;3(1):45.

15. Sherub S, Bohrer G, Wikelski M, Weinzierl R. Behavioural adaptations to flight into thin air. Biol Lett. 2016;12(10).

334    16.    Weinzierl R, Bohrer G, Kranstauber B, Fiedler W, Wikelski M, Flack A. Wind
335         estimation based on thermal soaring of birds. Ecol Evol. 2016;6:8706–18.

336    17.    Treep J, Bohrer G, Shamoun-Baranes J, Duriez O, Prata de Moraes Frasson J, Bouten
337         W. Using high-resolution GPS tracking data of bird flight for meteorological
338         observations. Bull Amer Meteor Soc. 2016;97:951–61.

339    18.    Taylor GK, Reynolds K V., Thomas ALR. soaring energetics and glide performance
340         in a moving atmosphere. Philos Trans R Soc Lond B Biol Sci. 2016;371(1704).

341    19.    Wood SN. Stable and efficient multiple smoothing parameter estimation for
342         generalized additive models. J Am Stat Assoc. 2004;99:673–86.

343    20.    Wood SN. mgcv R-software package. 2017.

344    21.    Kruuk H. Competition For Food Between Vultures in East Africa. Ardea. 1967;55(3–
345         4):171–93.

346    22.    Houston DC. Food Searching in Griffon Vultures. Afr J Ecol. 1974;12:63–77.

347    23.    Vansteelant WMG, Shamoun-Baranes J, McLaren J, van Diermen J, Bouten W.
348         Soaring across continents: decsion-making of a soaring migrant under changing
349         atmospheric conditions along an entire flyway. J Avian Biol. 2017;Online.

350    24.    Harel R, Duriez O, Spiegel O, Fluhr J, Horvitz N, Getz WM, et al. Decision-making
351         by a soaring bird: time, energy and risk considerations at different spatio-temporal
352         scales. Philos Trans R Soc London B Biol Sci. 2016;371(20150397).

353    25.    Akos Z, Nagy M, Vicsek T. Comparing birdand human soaring strategies. Proc Natl
354         Acad Sci U S A. 2008;105(11).

355    26.    Pennycuick CJ. Gliding flight of the white-backed vulture Gyps Africanus. J Exp Biol.
356         1971;55:13–38.

357    27.    Hedenström A, Alerstam T. Optimal flight speed of birds. Philos Trans R Soc B.
358         1995;348:471–87.

359    28.    Jackson AL, Ruxton GD, Houston DC. The effect of social facilitation on foraging
360         success in vultures: a modelling study. Biol Lett. 2008;4(3):311–3.

361    29.    Cortes-Avizanda A, Jovani R, Antonio D, Grimm V. Bird sky networks: How do
362         avian scavengers use social information to find carrion? Ecology. 2014;95(7):1799–
363         808.

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

366    31.    Harel R, Horvitz N, Nathan R. adult vultures outperform juveniles in challenging
367         thermal soaring conditions. Sci Rep. 2016;6(27867).

368    32.    Valone TJ, Templeton JJ. public information for the assessment of quality: a
369         widespreed social phenomenon. Philos Trans R Soc Lond B Biol Sci. 2002;357:1549–
370         57.

371    33.    Maurer V, Kalthoff N, Wieser A, Kohler M, Mauder M, Gantner L. Observed
372         spatiotemporal variability of boundary-layer turbulence over flat, heterogeneous
373         terrain. Atmos Chem Phys. 2016;16:1377–400.

374    34.    Nagy M, Couzin ID, Fiedler W, Wikelski M, Flack A. Synchronization, coordination
375         and collective sensing during thermalling flight of freely migrating white storks.
376         Philos Trans R Soc B. 2018;373(1746):20170011.

377    35.    Harel R, Spiegel O, Getz WM, Nathan R. Social foraging and individual consistency
378         in following behaviour: testing the information centre hypothesis in free-ranging
379         vultures. Proc R Soc B Biol Sci. 2017;284(1852).

380    36.    Lentink D, Müller UK, Stamhuis EJ, de Kat R, van Gestel W, Veldhuis LLM, et al.

381       How swifts control their glide performance with morphing wings. Nature.
382       2007;446:1082–5.

383

384

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 kg.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).

391

392

| Vulture (age) | Biometrics | ITG (s) | Theoretical optima | $V_a$ (m/s) | $V_a$ Regression |
|---|---|---|---|---|---|
| *G. fulvus* **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 | $V_a = 0.0022P_{volts} - 5.33$ |
| *G. fulvus* **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 | $V_a = 0.0063P_{volts} - 41.56$ |
| *G. fulvus* **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 | $V_a = 0.0056P_{volts} - 36.65$ |
| *G. himalayensis* **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 | $V_a = 0.0045P_{volts} - 26.42$ |
| *G. himalayensis* **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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394

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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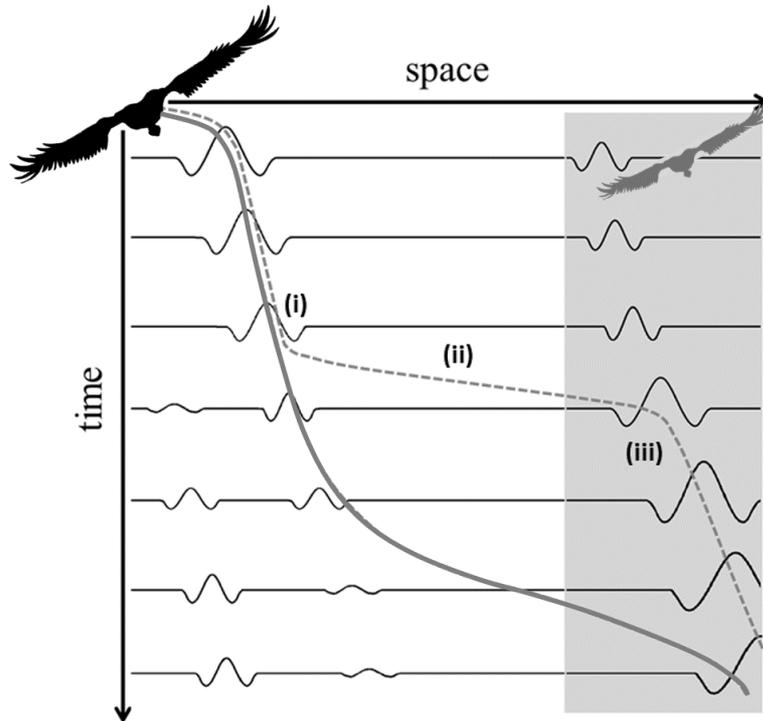
**Figure 1. The potential value of social information in aiding route selection in a dynamic environment.** Each horizontal line represents a moment in time along a trajectory in 2-dimensional space. The variation about the horizontal for each line represents the vertical velocity of the air; so that 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.
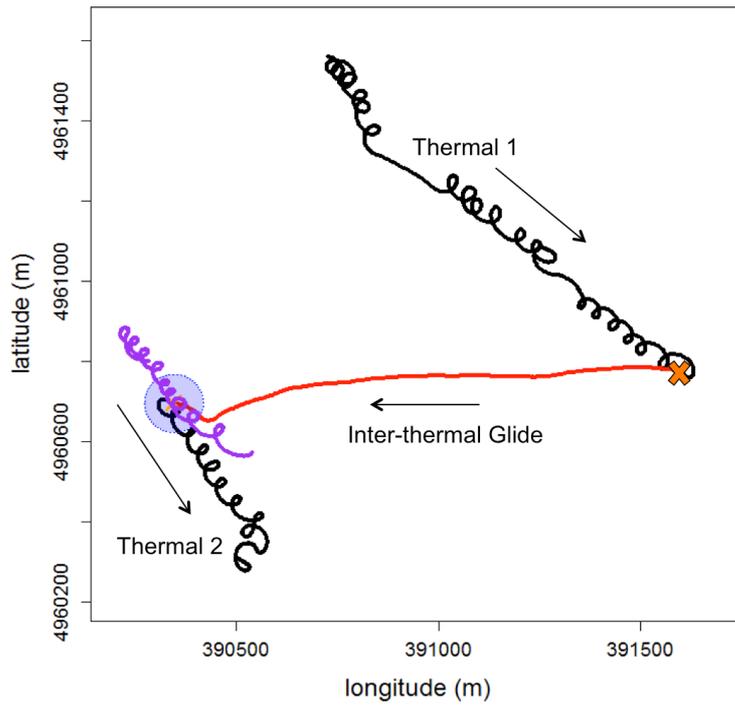
**Figure 2: The 2-dimensional track of a socially-informed glide (red) between two thermal soaring periods (black)**. The start of the glide is highlighted (orange cross), along with the radius (blue circle) used to identify spatial overlap in soaring behaviour. The soaring of a second vulture (purple 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.

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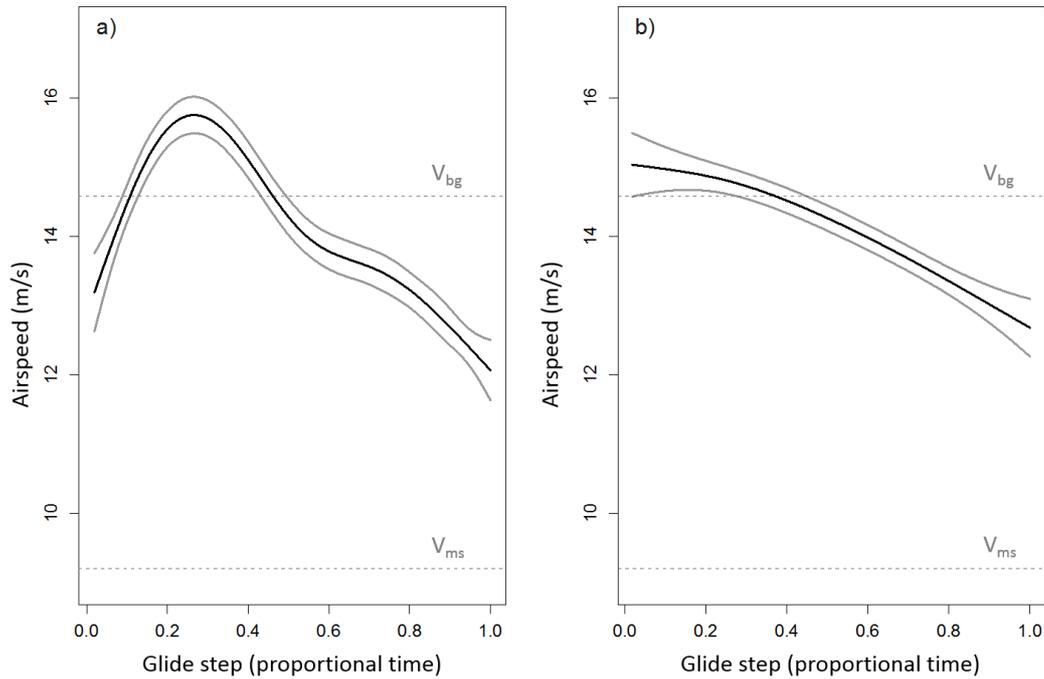
**Figure 3: Airspeed varied with time through the glide and access to social information.**
The pattern of decreasing airspeed through the glide was predicted by the smoothed component
of the GAMM in interaction with glide type. The form of this general decrease differed between
a) non-social (EDF = 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.