INTERFACE

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

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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 recognized 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 stylized 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 (approx. 3 m s ^{1}) 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.

Research

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1. Introduction

Individuals require up-to-date information about their environment to optimize their movement strategies [1–3]. Such information is particularly valuable for flying animals as not only is the aerial environment highly dynamic [4], but also 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× RMR (e.g. [5]). Large birds are therefore subject to strong selective pressure to locate and exploit updrafts as a means of subsidizing 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 unmanned aerial vehicles 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

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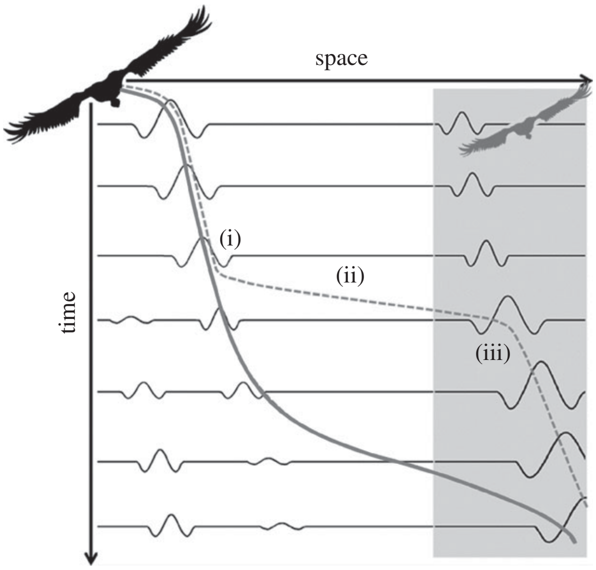

Figure 1. The potential value of social information in aiding route selection in a dynamic environment. Each horizontal line represents a moment in time along a trajectory in two-dimensional space. The variation about the horizontal for each line represents the vertical velocity of the air, so that a 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.

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 owing to the challenges in (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.

2. 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 (three adults and two immatures; table 1), and staggered by 5 min, 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 nine group flights (i.e. three flights on three 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, see [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 three 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 s, 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 1 hPa or 1 mbar). As the GPS unit took fixes at 4 Hz, all data were analysed at 4 Hz and duplicate time stamps in the GPS data were removed. This experimental set-up 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 the electronic supplementary material, 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 were taken as the points when birds either stopped or started circling within the thermal updraft, respectively, as identified using the magnetometry data (cf. [14]; electronic supplementary material, 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 (out 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 (s.d.; range 0.59) compared with 0.56 ± 0.34 (s.d.; 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 ± s.d.) to 98 ± 42 s for each bird.

2.1. 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 s periods of straight-line flight (defined as zero tortuosity) in the subsequent glide ($n = 294$), according to

$$V_a^2 = V_g^2 + V_w^2 + 2V_g V_w \cos\gamma, \tag{2.1}$$

where V_g is the mean ground speed vector for the 5 s and γ is the angle between ground- and wind-speed vectors. We performed linear regressions to predict the airspeed (m s^{-1}) from the Pitot

Table 1. Biometrics and gliding airspeeds for individual vultures. Birds showed inter-individual differences in airspeeds (V_a) through the glide ($F = 214.1_{10410,4}$, $p < 0.001$) 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 and durations of inter-thermal glides (ITGs) performed by the bird that were defined as uninformed (S1) and informed (S2).

vulture (age)	biometrics	ITG (s)	theoretical optima	V_a (m s^{-1})	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^{-1} V_{ms}: 9.20 m s^{-1}	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^{-1} V_{ms}: 8.80 m s^{-1}	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^{-1} V_{ms}: 8.70 m s^{-1}	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^{-1} V_{ms}: 8.70 m s^{-1}	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^{-1} V_{ms}: 8.70 m s^{-1}	16.56 ± 3.47	V_a	$0.0047P_{volts}$	28.33

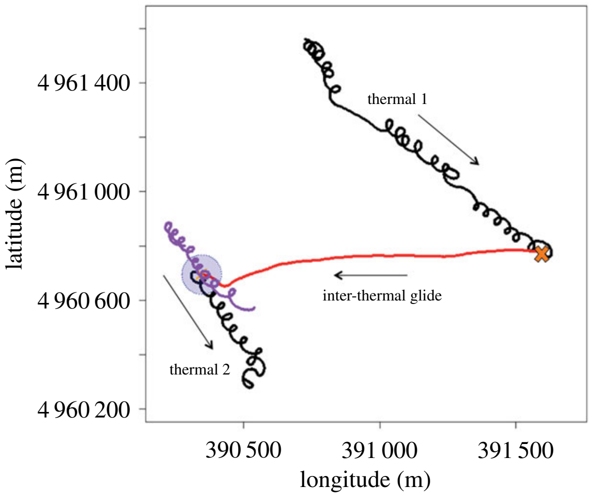

Figure 2. The two-dimensional track of a socially informed glide (red) between two thermal-soaring periods (black). The start of the glide is highlighted (orange cross), along with the radius (purple circle) used to identify spatial overlap in soaring behaviour. The soaring of a second vulture (purple 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.

tube output (volts) for these straight glide periods (table 1) and used the regression output to convert volts to metres per second for each datum point along the entire glide.

2.2. Social information in inter-thermal glides

Each glide was divided into continuous 3 s 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 five individuals ($N = 35$) were defined as either socially informed or uninformed 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 two time steps of the glide (figure 2). This two-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.

2.3. 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* condition 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 nine (mgcv R-software package [19,20]). The *headwind* component, previous *climb* rate and starting *altitude* were included as

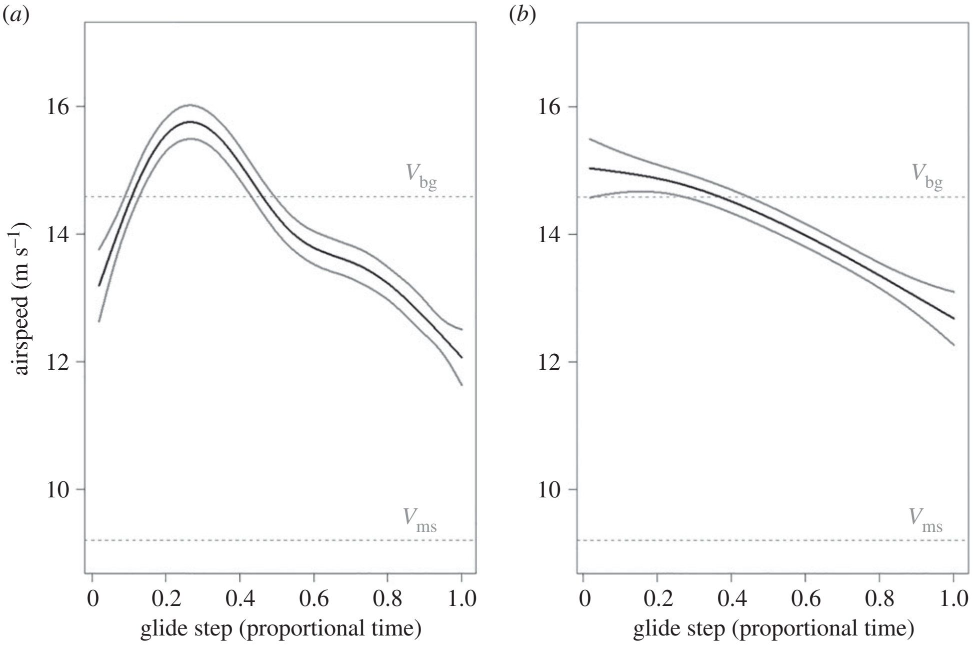

Figure 3. Airspeed varied with time through the glide and access to social information. The pattern of decreasing airspeed through the glide was predicted by the smoothed component of the GAMM in interaction with glide type. The form of this general decrease differed between (*a*) uninformed (EDF $= 5.91$, $F = 60.08$, $p < 0.001$, $n = 599$) and (*b*) informed 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.

continuous linear terms. The *headwind* component (V_h) was calculated according to

$$V_h = V_w \cos\theta, \tag{2.2}$$

where V_w is the wind vector and θ is 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^{-1}) 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 v. 3.3.1).

3. Results

At the point when birds began their inter-thermal glides (*glide step* $\leq$0.05), those with social information on the location of the next thermal had significantly higher airspeeds (17.0 m s^{1}) than those without (15.8 m s^{1}) ($t = -2.25$, d.f. $= 15.46$, $p = 0.034$). 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 ($t = -0.149$, d.f. $= 15.5$, $p = 0.884$, *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 approximately 12 m s^{1} at the end of the glide (*informed* $= 12.7 \pm 0.4$ m s^{1}, *uninformed* $=$ 12.1 ± 0.4 m s^{1}) (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.

4. 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 and figure 3), and in a manner that aligns with aeronautical predictions [9]. At the start of the glide, birds with access to social information adopted higher airspeeds (17.0 m s^{1}) than those relying on personal information (15.8 m s^{1}). 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 categorized 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 relatively quickly. The increase in speed part way through the glide by uninformed birds (the peak speed at 25% through the glide; figure 3) likely represents a response to this downdraft, with the 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],

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; gam) 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.

lme	estimate	s.e.	*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	

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 approx. 12 m s^{-1}; 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 (approx. 3 m s^{-1}). 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 maximize distance gained per unit of altitude lost; here that difference is approx. 4.5 m s^{-1}) [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 prioritize, be it maximizing the distance flown or minimizing 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 (see [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^{-1} compared with 0.4 ± 0.7 m s^{-1} for birds soaring 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 time scales 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 time scales, 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, France). Birds were handled by their usual trainer, under the permit of the Rocher des Aigles.

Data accessibility. 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.

Authors' contributions. The study was conceived and the article drafted by H.J.W., E.L.C.S. and A.J.K. Data were collected by H.W. and O.D., and analysed by H.W. with input from all authors. All authors critically revised the manuscript.

Competing interests. The authors declare no competing interests.

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References

1. Rafacz M, Templeton JJ. 2003 Environmental unpredictability and the value of social information for foraging starlings. *Ethology* **109**, 951–960. (doi:10.1046/j.0179-1613.2003.00935.x)
2. Dechmann DKN, Heucke SL, Giuggioli L, Safi K, Voigt CC, Wikelski M. 2009 Experimental evidence for group hunting via eavesdropping in echolocating. *Proc. R. Soc. B* **276**, 2721–2728. (doi:10.1098/rspb.2009.0473)
3. Dall SRX, Giraldeau L, Olsson O, Mcnamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)
4. Shepard ELC, Ross AN, Portugal SJ. 2016 Moving in a moving medium: new perspectives on flight. *Phil. Trans. R. Soc. B* **371**, 20150382. (doi:10.1098/rstb.2015.0382)
5. Elliott KH, Ricklefs RE, Gaston AJ, Hatch SA, Speakman JR, Davoren GK. 2013 High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci. USA* **110**, 9380–9384. (doi:10.1073/pnas.1304838110)
6. Stolle M, Bolting J, Döll C, Watanabe Y. 2015 A vision-based flight guidance and navigation system for autonomous cross-country soaring UAVs. In *Proc. ICUAS 2015—Int. Conf. on Unmanned Aircraft Systems, Denver, CO, 9–12 June 2015*. New York, NY: IEEE.
7. Pennycuick CJ. 1972 Soaring behaviour and performance of some East African birds observed from a motor-glider. *Ibis* (*Lond 1859*). **114**, 178–218. (doi:10.1111/j.1474-919X.1972.tb02603.x)
8. Pennycuick CJ. 2008 *Modelling the flying bird*, vol. 5. Boston, MA: Elsevier.
9. van Loon EE, Shamoun-Baranes J, Bouten W, Davis SL. 2011 Understanding soaring bird migration through interactions and decisions at the individual level. *J. Theor. Biol.* **270**, 112–126. (doi:10.1016/j.jtbi.2010.10.038)
10. MacCready PB. 1958 Optimum airspeed selector. *Soaring* **January–February**, 10–11.
11. Horvitz N, Sapir N, Liechti F, Avissar R, Mahrer I, Nathan R. 2014 The gliding speed of migrating birds: slow and safe or fast and risky? *Ecol. Lett.* **17**, 670–679. (doi:10.1111/ele.12268)
12. Flack A, Nagy M, Fiedler W, Couzin ID, Wikelski M. 2018 From local collective behaivour to global migratory patterns in white storks. *Science* **360**, 911–914. (doi:10.1126/science.aap7781)
13. Wilson RP, Shepard ELC, Liebsch N. 2008 Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang. Species Res.* **4**, 123–137. (doi:10.3354/esr00064)
14. Williams HJ, Shepard ELC, Duriez O, Lambertucci SA. 2015 Can accelerometry be used to distinguish between flight types in soaring birds? *Anim. Biotelemetry. BioMed. Central.* **3**, 45. (doi:10.1186/s40317-015-0077-0)
15. Sherub S, Bohrer G, Wikelski M, Weinzierl R. 2016 Behavioural adaptations to flight into thin air. *Biol. Lett.* **12**, 20160432. (doi:10.1098/rsbl.2016.0432)
16. Weinzierl R, Bohrer G, Kranstauber B, Fiedler W, Wikelski M, Flack A. 2016 Wind estimation based on thermal soaring of birds. *Ecol. Evol.* **6**, 8706–8718. (doi:10.1002/ece3.2585)
17. Treep J, Bohrer G, Shamoun-Baranes J, Duriez O, Prata de Moraes Frasson R, Bouten W. 2016 Using high-resolution GPS tracking data of bird flight for meteorological observations. *Bull. Amer. Meteorol. Soc.* **97**, 951–961. (doi:10.1175/BAMS-D-14-00234.1)
18. Taylor GK, Reynolds KV, Thomas ALR. 2016 Soaring energetics and glide performance in a moving atmosphere. *Phil. Trans. R. Soc. B* **371**, 20150398. (doi:10.1098/rstb.2015.0398)
19. Wood SN. 2004 Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J Am Stat Assoc.* **99**, 673–686. (doi:10.1198/016214504000000980)
20. Wood SN. 2017 mgcv R-software package. See https://cran.r-project.org/web/packages/mgcv/mgcv.pdf.
21. Kruuk H. 1967 Competition for food between vultures in East Africa. *Ardea* **55**, 171–193.
22. Houston DC. 1974 Food searching in griffon vultures. *Afr. J. Ecol.* **12**, 63–77. (doi:10.1111/j.1365-2028.1974.tb00107.x)
23. Vansteelant WMG, Shamoun-Baranes J, McLaren J, van Diermen J, Bouten W. 2017 Soaring across continents: decsion-making of a soaring migrant under changing atmospheric conditions along an entire flyway. *J. Avian Biol.* **48**, 887–896. (doi:10.1111/jav.01298)
24. Harel R *et al.* 2016 Decision-making by a soaring bird: time, energy and risk considerations at different spatio-temporal scales. *Phil. Trans. R. Soc. B* **371**, 20150397. (doi:10.1098/rstb.2015.0397)
25. Akos Z, Nagy M, Vicsek T. 2008 Comparing bird and human soaring strategies. *Proc. Natl Acad. Sci. USA* **105**, 4139–4143. (doi:10.1073/pnas.0707711105)
26. Pennycuick CJ. 1971 Gliding flight of the white-backed vulture Gyps africanus. *J. Exp. Biol.* **55**, 13–38.
27. Hedenström A, Alerstam T. 1995 Optimal flight speed of birds. *Phil. Trans. R. Soc. B* **348**, 471–487. (doi:10.1098/rstb.1995.0082)
28. Jackson AL, Ruxton GD, Houston DC. 2008 The effect of social facilitation on foraging success in vultures: a modelling study. *Biol. Lett.* **4**, 311–313. (doi:10.1098/rsbl.2008.0038)
29. Cortes-Avizanda A, Jovani R, Antonio D, Grimm V. 2014 Bird sky networks: how do avian scavengers use social information to find carrion? *Ecology* **95**, 1799–1808. (doi:10.1890/13-0574.1)
30. Fischer AB. 1969 *Laboratory experiements on, and open-country observations of the visual acuity and behaviour, of old world vultures*. Muenster, Germany: University of Muenster.
31. Harel R, Horvitz N, Nathan R. 2016 Adult vultures outperform juveniles in challenging thermal soaring conditions. *Sci. Rep.* **6**, 27867. (doi:10.1038/srep27865)
32. Valone TJ, Templeton JJ. 2002 Public information for the assessment of quality: a widespread social phenomenon. *Phil. Trans. R.*

Soc. Lond. B **357**, 1549 – 1557. (doi:10.1098/rstb.2002.1064)

33. Maurer V, Kalthoff N, Wieser A, Kohler M, Mauder M, Gantner L. 2016 Observed spatiotemporal variability of boundary-layer turbulence over flat, heterogeneous terrain. *ASTM Spec. Tech. Publ.* **16**, 1377 – 1400. (doi:10.5194/acp-16-1377-2016)
34. Nagy M, Couzin ID, Fiedler W, Wikelski M, Flack A. 2018 Synchronization, coordination and collective sensing during thermalling flight of freely migrating white storks. *Phil. Trans. R. Soc. B* **373**, 20170011. (doi:10.1098/rstb.2017.0011)
35. Harel R, Spiegel O, Getz WM, Nathan R. 2017 Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. *Proc. R. Soc. B* **284**, 20162654. (doi:10.1098/rspb.2016.2654)
36. Lentink D *et al.* 2007 How swifts control their glide performance with morphing wings. *Nature* **446**, 1082 – 1085. (doi:10.1038/nature05733)