RESEARCH ARTICLE

The characteristic time-scale of perceived information for decision-making: Departure from thermal columns in soaring birds

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Abstract

1. Animals are often required to make decisions about their use of current resources while minimising travel costs and risks due to uncertainty about the forthcoming resources. Passive soaring birds utilise warm rising-air columns (thermals) to climb up and obtain potential energy for flying across large areas. However, the utilisation of such inconsistent natural resources may be challenging for soaring-gliding birds and involve a set of decisions to maintain efficient flight.

2. To assess which temporal scales of previous experience with environmental inputs best predicted thermal-climbing departure decisions of soaring birds, we used movement data from Eurasian griffon vultures (*Gyps fulvus*) tracked by GPS transmitters. We applied Cox proportional hazard regression and a model selection approach to identify thermal-climbing departure decisions and to compare a range of temporal scales.

3. Our findings support the use of current and recent (short-term; last 20 min) experiences, compared to longer term, past experiences, in predicting the time until departure from thermals. The models supported decision rules that integrated information originating from different temporal scales, implying a tendency to depart from a thermal later when the current climb rate was higher than experienced recently and vice versa. In addition, climb rates in thermals revealed significant autocorrelation over short time-scales (shorter than 30 min).

4. The correspondence between thermals' characteristics and the factors that best predicted thermal-climbing departure decisions presumably reflects optimal decisions individuals make to handle their dynamic environment and to reduce movement-related costs of such a basic activity for soaring-gliding birds.

KEYWORDS
bayesian forager, flight, gyps fulvus, memory, patch departure, soaring-gliding, trade-off

1 | INTRODUCTION

While climbing a warm rising-air column (thermal), soaring birds need to balance too early departure (waste of climbing opportunity) against too late departure (waste of time with no further significant displacement), given the uncertainty about the thermal ahead. Such

decisions that deal with where and when individuals move affect energy reservoirs and determine the accompanying costs of movement (Alerstam & Lindström, 1990; Nathan et al., 2008; Shepard et al., 2013). The use of passive soaring instead of self-powered flight affects locomotion costs, as passive soaring costs 3–20 times less than self-powered flight (Sapir, Wikelski, McCue, Pinshow, &

Nathan, 2010; Videler, 2006). However, compared to self-powered flight, passive soaring incurs dependency on strong thermals that exhibit inconsistent variation between nearby thermals and within single thermals (Hedenström, 2003; Reichmann, 1978). Therefore, passive soaring birds routinely perform time-related decisions to remain aloft and maintain efficient search for their food resources.

Due to the challenge in gathering high-resolution data to estimate the characteristics of the different phases of passive soaring, most previous studies coupled soaring and gliding decisions and estimated time-related costs over large scales (Klaassen et al., 2014; Mellone et al., 2012; Miller et al., 2016; Rus, Duerr, Miller, Belthoff, & Katzner, 2017; Shamoun-Baranes, Baharad, et al., 2003; Shamoun-Baranes, Leshem, Yom-tov, & Liechti, 2003; Vansteelant et al., 2015). However, the characterisation of the different phases of passive soaring enabled further insights on the different decisions individuals make. In the gliding phase, individuals choose how quickly to glide forward while exploiting the potential energy gained during thermal climbing (Harel, Duriez, et al., 2016; Hedenstrom & Alerstam, 1995; Horvitz et al., 2014; Pennycuick, 1972; Pennycuick, Akesson, & Hedenström, 2013; Taylor, Reynolds, Thomas, & Taylor, 2016). Variation in the resulting gliding speed was explained by differences in individual's environment (Horvitz et al., 2014; Taylor et al., 2016), as well as by intraspecific (Harel, Duriez, et al., 2016; Taylor et al., 2016) and interspecific variation (Horvitz et al., 2014; Pennycuick, 1972; Pennycuick et al., 2013). After a thermal column was spotted, individuals decide whether to use it, how to best utilise it (Harel, Horvitz, & Nathan, 2016) and when to depart (Shepard, Lambertucci, Vallmitjana, & Wilson, 2011). Soaring-gliding birds are expected to maximise soaring–gliding efficiency and cross-country speed by minimising the duration of stay in thermal columns in relation to the horizontal forward gain during the gliding phase (Harel, Duriez, et al., 2016; Reichmann, 1978). However, additional considerations may affect decisions of soaring birds, such as a preference to fly at higher altitudes above-ground level to avoid risk of grounding (Horvitz et al., 2014; Reichmann, 1978) or the need to balance the gain from thermal columns while being bounded by the need to identify food items that are located on the ground (Shepard et al., 2011).

The study of the factors that determine departure decisions from patchy resources typically used information over a restricted time span or was based on the assumption that individuals possess complete information hence presenting an extreme and rather unrealistic scenario of such decision-making processes. Further insights can be gained by comparing models that implement different levels of information on the environment (Marshall, Carter, Ashford, Rowcliffe, & Cowlishaw, 2013). Relevant information may be based on different characteristics of the environment (e.g. depletion rate, resource quality, patch density) that may differ in the characteristic time period over which inputs are considered to produce profitable decisions. Alternative scenarios for soaring-gliding decisions may include information collected over different time periods, such as (I) *Current experience*. Thermal-climbing departure decisions may follow fixed rules, such as amount of gained energy or time spent in the

current thermal (Nolet, Klaassen, & Mooij, 2006; Olsson & Brown, 2006). The gathered information can include different aspects, such as the achieved climb rate which individuals aim to maximise and the entrance altitude into the thermal. (II) *Recent experiences*. Individuals update their decisions using their recent experiences (learning rule models; Kacelnik & Krebs, 1985) or combine information from their recent experiences with current one (Bayesian forager; Green, 1984; McNamara, Green, & Olsson, 2006). These models assume that foragers routinely update their perception of the distribution of resources. However, the extent of spatial and temporal perception is understudied for free-ranging animals (Fagan et al., 2013). (III) *Long-term experiences*. Daily or longer term averages were commonly used to evaluate the effect of environment on behaviour due to challenges in tracking animals and documenting the relevant environmental factors that affect movement. Such experiences may be global ones (the expected gain in a given day is better than a long-term average) or may be spatially associated (usually the expected gain is high at the current location). This latter approach typically reflects data limitation rather than best choice scenario.

Here, we studied thermal-climbing departure decisions by a large scavenger, the Eurasian griffon vulture (*Gyps fulvus*). To estimate which factors best predict thermal-climbing departure, we compared models incorporating information collected over different spatiotemporal scales considering current, recent and long-term experiences. We hypothesised that thermal-climbing departure decisions would be based on current experiences because information regarding the current thermal may be more valid compared to the prior thermals and due to the unpredictable nature of thermal columns (Reichmann, 1978). Focusing on the current experience, we predicted that the tendency to depart from a thermal would increase with an increased thermal entrance altitude and average climb rate. To estimate the characteristic time-scale of the performed decisions, we tested which set of recent thermals best predicted thermal-climbing departure. To evaluate the effect of the context in which animals are found on their decisions, we also tested how thermal departure depends on additional internal factors, such as the effect of familiarity with the area, distance from the roost (changes in certainty regarding movement outcomes), age and differences between inbound and outbound foraging flights (sensu Harel, Duriez, et al., 2016) that differ in their motivation.

2 | MATERIALS AND METHODS

2.1 | Study species and data collection

The Eurasian griffon vulture (*Gyps fulvus*; Hablizl 1783) is a large scavenger (mass: ~7.5 kg; wingspan span: ~2.6 m) that usually uses thermal climbing (Harel, Horvitz, et al., 2016) and seldom uses powered flight (Cramp, 1985; Mundy, Butchart, Ledger, & Piper, 1992). Between 2013 and 2015, seventeen individuals were tracked with 90 g GPS transmitters (e-obs GmbH; Munich, Germany). The transmitters were programmed to work with a daily duty cycle of 14 hr (6:00–20:00 local time) collecting location data at 1 Hz during flight

(when the measured instantaneous speed was >2 m/s) and at 600-s intervals on the ground. Soaring phases were classified as segments that contained circling behaviour (defined based on circles in the horizontal plane of the track) and a positive altitudinal gain. Segments with gaps longer than 10 s were excluded, and each soaring segment was classified to one of two soaring modes: thermal soaring or linear soaring (see Harel, Horvitz, et al., 2016; Weinzierl et al., 2016). In some cases, individuals may stop circling for a short period and perform short glides to displace within the thermal column; therefore, we grouped closely spaced thermal-climbing events (<30 s between events; within-thermal short glides); groupings accounted for ~10% of the events. Due to our limited ability to estimate thermal strength (Treep et al., 2016), we used climb rate as an indirect measure of the estimated gain from a resource visited by an individual. Because thermal-climbing events were defined by the behaviour of individuals and not based on measuring the thermal strength itself, we tested different parameters of within-thermal short glides (0–50 s) and no significant effects were observed on the duration, climb rate and thermal-climbing entrance altitude (Supporting Information Table S1). The data used in this study are available from the Movebank Data Repository (Harel & Nathan, 2018).

2.2 | Data analysis

We used mixed-effects Cox Proportional Hazard models and a multinomial framework to estimate the factors and the temporal scale that best predicted time to a thermal-climbing departure event. In the Cox models, the hazard of lower survival (i.e. a shorter event) is modelled in proportion to a reference event in a multiplicative manner, meaning that for a positive or negative change Z in the predictor,

the event is Z-times shorter or longer, respectively, than the reference event. In our application of this model for soaring vultures, the hazard of having a shorter event means earlier departure from a thermal. In a more specific manner, hazard ratios >1 indicate that a given change Z in the predictor (e.g. climb rate) is associated with Z-times earlier departure from the thermal compared to a reference event (e.g. thermal climbing at an average climb rate), while values <1 represent a tendency to depart later. For example, a hazard ratio of 1.2 means that for this particular predictor value, the thermal-climbing event is 20% shorter than the thermal-climbing duration when vultures climb at an average rate.

The compared models included characteristics of the (A) current experience (focal event): initial altitude, the average climb rate and its variance over the whole soaring phase, the running average climb rate and its variance over the last n seconds (n = 5, 10, ..., 120) in the soaring phase; (B) recent experiences (short-term): average climb rate and average duration of the thermal-climbing events during the last k minutes (k = 10, 15,..., 90 min); (C) long-term experiences: daily climb average and its variance, daily average of soaring duration and resource quality based on the average climb rate of all the tracked individuals in the vicinity of the event (2 km^2) during the last 7 days (Figure 1d); (D) context: spatial familiarity based on the amount of visits to the relevant location (2 km^2; Figure 1c); age (categorical factor; years; <1, juvenile; 1> and <4, sub-adult; >4, adult); time of day (categorical factor with three levels 7:00–10:00, 10:00–13:00, 13:00–16:00); distance from the roost and to the goal site; and distance between the start and end point of the current flight and whether the flight was an inbound or outbound foraging flight; individual's identity was added as a random effect. For each of the models (A–D), we established the best fitting model, identified the best fitting temporal scale and then compared 15 models that included
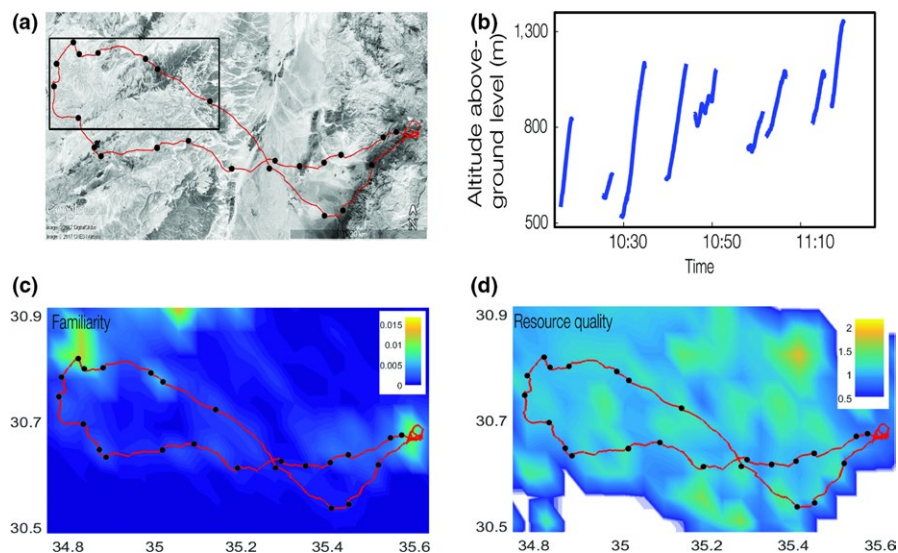

FIGURE 1 An example of a foraging track (tag 3,186 on September 2nd, 2013). (a) The flight track (red line) and the locations of thermal-climbing events (black circles) are presented. (b) The altitude profiles of a subset of the track (marked by the black square in (a)). The context and long-term experiences are presented by (c) the familiarity index which summarises the proportion of visits to a cell grid within the last week (colour bar represents the proportion of visits of the bird), and (d) the resource quality measured by the average climb rate for a cell based on the data from all tracked individuals during the last week. The red lines in (c) and (d) represent the track for reference

TABLE 1 Results of Cox Proportional Hazard model comparison on time to thermal-climbing departure decision

	df	logLik	AIC$_c$	Delta	Weight
Current (alt, climb); *Recent experience* (alt, climb, dur); *Context* (goal_dist)	22	−20,268	40,582	0	0.92
Current (alt, climb); *Recent experience* (alt, climb, dur); *Long-term experience* (climb); *Context* (goal_dist, daily_dist, in_out, age)	30	−20,263	40,587	5	0.08
Current (alt, climb); *Long-term experience* (climb)	21	−20,394	40,831	249	0.00
Current (alt, climb)	20	−20,396	40,834	251	0.00
Recent experience (alt, climb, dur)	21	−20,467	40,978	395	0.00
Context (goal_dist, daily_dist, in_out, age)	18	−22,009	44,056	3,473	0.00
Intercept only	12	−22,026	44,079	3,496	0.00

Notes. All models presented include individual identity as a random effect.

AIC$_c$, Akaike's Information Criterion; alt, thermal entrance altitude above-ground level; climb, climb rate (m/s); dur, event duration (s); goal_dist, distance from goal; daily_dist, daily flight distance; in_out, inbound or outbound foraging flight; age, categorical.

the chosen predictors from the different model types (Supporting Information Table S2).

Data were analysed using Matlab2016a (MathWorks Inc, Natick, MA, USA). Statistical analyses were performed using R v.3.2.2 statistical software (R Core Team 2017) with LME4 (Bates, Maechler, Bolker, & Walker, 2014) and COXME (Therneau, 2012) packages. Models were ranked based on small-sample-size corrected Akaike's Information Criterion.

3 | RESULTS

Data included 14 ± 2 foraging days for each of the 17 tracked individuals in which the daily travel distance was 132 ± 1 km covered in 4.6 ± 0.8 hr (values are presented as mean ± *SE*; see Figure 1 for an example of a daily flight path). On those foraging trips, individuals performed 22.8 ± 0.7 soaring-gliding cycles per day, and ~5,400 cycles overall. The duration of each thermal-climbing event was 207 ± 11 s and each gliding event lasted 134 ± 88 s.

To assess which factors best predicted thermal-climbing departure, a set of models describing current, recent and long-term experiences and the context of the event were compared (see Supporting Information Table S2 for a full list of the models). The best fitting model integrated predictors which were derived from current and recent experiences, as well as the context of the event (Table 1). As expected, the tendency to depart from a thermal increased with an increase in the initial altitude of the thermal-climbing event (0.0009 ± 0.00006, Z-wald = 14.56; here and hereafter, the given effect size represents the partial hazard ratio). Moreover, an increase in the mean climb rate of the current thermal-climbing event resulted in a lower tendency to depart (0.37 ± 0.04, Z-wald = 9.39). The effect of recent experiences revealed a higher tendency to depart from the thermal earlier when there was an increase in the mean climb rate of recent thermals (Figure 2b). When individuals were in proximity of their roost (<4 km), the hazard ratio was lower compared to flights further from the roost (−0.14 ± 0.04, Z-wald = 3.69), but

the inclusion of the overall familiarity with the habitat (amount of visits to each location) did not improve the predictive power of the models.

Focusing on the recent experiences of the individual, the partial autocorrelation of the climb rate showed significant values over short periods (10–30 min; Figure 1c) but not over longer ones (40–90 min). According to that, the characteristics of the recent thermal-climbing events within the last 20 min best predicted time to thermal-climbing departure compared to shorter and longer time periods (10–90 min; Table 2). Incorporating daily averages of the climb rate or average resource quality over longer periods (average weekly climb rate of the location of the thermal-climbing event) did not improve the predictive power of the models compared to recent experience models (Figure 2). The best model integrated the effect of current and recent experiences predicting a tendency to depart early from the thermal when the current climb rate was stronger than the average of those experienced during the last 20 min and vice versa (0.56 ± 0.03, Z-wald = 16.11; Figure 3b).

4 | DISCUSSION

The characteristic time-scale of decision-making in animals moving in complex real-life environments is often unknown. Large soaring birds, such as vultures, fly long distances by utilising thermals to climb up and gain potential energy for forward movement. Vultures use thermals intensively, hence, they likely rely on using various types of information inputs to make efficient decisions on the use of such a patchy and highly unpredictable resource. Using high-resolution data on vulture movements and their environment, we found that information collected over current and recent experiences best predicted thermal-climbing departure decisions, outperforming alternative models that were based on the sole use of current or long-term experiences. Overall, our findings bring to light how vultures, and possibly other large soaring birds, integrate fine-scale differences in their environment, including flight altitude and climb rate, while making decisions regarding when and where to move.
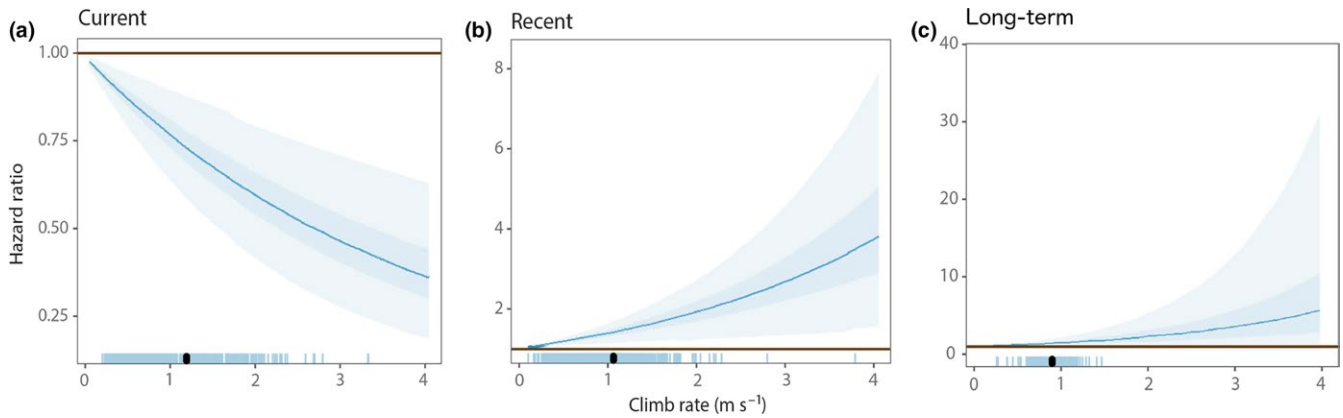
FIGURE 2 The effect of the average climb rate at different temporal scales on thermal-climbing duration. The partial hazard ratio of the climb rate for (a) current thermal suggesting early departure, (b) for recent 20 min (or ~3 thermals) suggesting late departure. Averages over longer durations, such as (c) the daily scale, were not significantly different from one another, suggesting no significant effect (based on the results of the best fitting model; see Table 1). For a given change in the predictor (here climb rate), the duration of the predicted thermal-climbing departure event should be multiplied by the calculated hazard ratio. Hazard ratio values >1 indicate a tendency to depart earlier from the event compared to departure time predicted for a reference event (climbing a thermal at an average climb rate), while values <1 indicate a tendency to depart later. Blue lines represent the mean value with 50% and 95% CIs around it. At the bottom of the figure, the occurrences of events and the average climb rates as reference values are presented

Previous research on soaring-gliding flight in birds focused on movement patterns over relatively long temporal scales of weeks and months, and large spatial scales of tens to thousands of kilometres (Bohrer et al., 2012; Mellone et al., 2012; Miller et al., 2016; Vansteelant et al., 2015). These studies aimed mostly at estimating how variation among species (Bohrer et al., 2012; Mellone et al., 2012) and in meteorological conditions (Miller et al., 2016; Vansteelant, Shamoun-Baranes, McLaren, van Diermen, & Bouten, 2017) can explain the observed variation in large-scale movement patterns (mostly migration). Although some of these studies were based on relatively high-resolution movement data (10–30 s intervals), the statistical analyses in these studies were performed at coarser temporal resolutions of 1 hr or more. Both the internal state of the tracked birds and their external environment can vary considerably within 1 hr or more, and birds are likely to make multiple decisions in response to these changes during such timeframes. Therefore, although these studies provided important insights about interspecific variation among soaring birds and how weather affects their large-scale migratory movements, the temporal resolution used in these analyses was too coarse to link specific decisions to
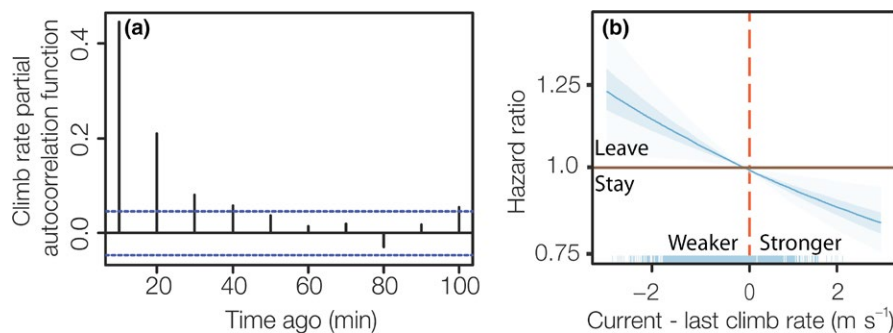
TABLE 2 The effect of the climb rate (averaged over several time windows) during previous experiences on time to thermal-climbing departure decision

	Effect	df	logLik	AIC$_c$	Delta	Weight
20 min	0.87	3	−209.2	424.4	0.0	1.00
10 min	0.89	3	−253.0	512.2	87.8	0.00
30 min	0.93	3	−272.5	551.1	126.7	0.00
40 min	0.93	3	−285.6	577.3	152.9	0.00
50 min	0.95	3	−292.3	590.7	166.3	0.00

Note. AIC$_c$, Akaike's Information Criterion.

FIGURE 3 The effect of recent experiences on thermal-climbing duration. (a) The partial autocorrelation function of the climb rate was significant over the thermal-climbing events during the 10–30 min excluding the focal event. (b) When the current climb rate was lower than the recent experiences, the partial hazard ratio was greater than one suggesting a higher tendency to depart and vice versa. At the bottom, the occurrences of events are presented. Blue lines represent the mean value with 50% and 95% CI around it. For information regarding hazard ratio interpretation, see the corresponding *Methods* section and the caption of Figure 2

certain sets of internal states and external conditions. Some other studies analysed movement data at high temporal resolution that is relevant to specific decisions (Horvitz et al., 2014; Pennycuick et al., 2013), thus narrowing the focus to decisions in response to rather short-term changes. Yet, these studies focused mostly on examining interspecific variation in-flight performance and hence incorporated complex effects that also impede elucidating the links between specific decisions and their internal and external drivers. Shepard et al. (2011) analysed movement data at high temporal resolution focusing on soaring flight and raising predictions that relate to the factors that govern flight altitude and thermal-climbing departure decisions; however, their sample size was too small to observe how decisions are affected by variation in environmental conditions. Our intraspecific comparison of thermal-climbing events of free-ranging vultures recorded at high temporal resolution and continued over sufficiently long periods illustrates a novel approach to uncover such links.

Our findings suggest that vultures integrated current and recent experiences (over the last 20 min or the previous three thermal-climbing events), whereas longer term experiences of the previous day or week were found irrelevant for thermal-climbing departure decisions. In that order, over 10–30 min, climb rates which served to estimate the uplift individuals achieved while soaring were positively correlated (Figure 3a). The correspondence between animals' decisions and the estimated characteristics of resources suggests that vultures utilised the resources in a profitable manner. While this is the first time such a pattern had been supported in soaring birds, similar findings were reported for foraging animals supporting the use of short-term memory (Marshall et al., 2013) and highlighted the preference for information gathered over short-term periods compared to longer ones (Strandburg-Peshkin, Farine, Crofoot, & Couzin, 2017), presumably because recently gathered information encompasses more relevant information on the current situation individuals are facing (Fagan et al., 2017). Due to the longevity of vultures, their starvation tolerance (Spiegel, Harel, Getz, & Nathan, 2013) and the large spatial ranges they frequently cover (Spiegel et al., 2015), we suggest that the exclusion of the long-term quality of the area surrounding the thermal-climbing event from the best fitting model was not due to limited capacity to handle spatial memory over these scales but because the gathered information was not beneficial over these scales (after a few dozens of minutes) (Fagan et al., 2017).

The concept of decision rules in ecology plays an important role when studying the way animals deal with uncertainty and complex environments (Fawcett et al., 2014). Such rules were used to describe different phenomena, including breeding dispersal decisions (Hoover, 2003), food patch departure decisions (Wajnberg, Fauvergue, & Pons, 2000) and mate-choice decisions (Dale & Slagsvold, 1996). Here, we suggest that vultures use the relative gain of the current thermal column event in relation to the average gain during the last few utilised thermal columns. We also observed that thermal-climbing departure decisions were affected by a series of factors other than climb rate, such as flight altitude and distance from the roost. The observed effect of flight altitude may reflect the need to visually locate food items on the ground (Shepard et al.,

2011). Other external factors, such as the added information regarding nearby resources derived from conspecifics may also affect in-flight decision-making, probably by decreasing thermal-climbing duration. Therefore, the decision to depart from a thermal column integrates a set of inputs which should be weighed against each other to produce a decision.

While Eurasian griffon vultures use mostly passive soaring flight, other bird species vary their use of powered and passive soaring flight (Shamoun-Baranes, Bouten, van Loon, Meijer, & Camphuysen, 2016; Taylor et al., 2016; Weimerskirch, Bishop, Jeanniard-du-Dot, Prudor, & Sachs, 2016). For species that change their flight mode frequently, the additional time-related decisions are likely related to the frequency of powered flight and the individual-specific power curve. Moreover, the study of variation in time-related decisions across other taxa or different habitats may enable to the understanding of the extent to which the characteristic time-scales identified could be generalised and may shed light on the nature of the dynamic environment soaring individuals face. Reliable information on the resources individuals face at the relevant spatiotemporal scale may assist us to gain a more mechanistic understanding of the significant decisions vultures make while soaring and to evaluate whether their decisions are optimal in the future. Nevertheless, the prevalent spatiotemporal heterogeneity and autocorrelation of resources characterising many real-world environments may promote consistent deviations from an accurate perception of the environment that may lead to maladaptive behaviours (Fawcett et al., 2014).

By quantifying fine-scale patterns of soaring-gliding flight, we were able to pinpoint the factors affecting decisions and the way animals face their uncertain environment. Furthermore, the fine-scale data enabled assessment of the characteristic time-scale of information used for decision-making, suggesting that vultures resolved the uncertainty characterising their surrounding resources by acting as Bayesian foragers (Green, 1984; McNamara et al., 2006). The mechanisms governing such decisions likely integrate different and possibly opposing inputs which should be weighted to determine the best option among possible alternatives (Stephens, 2008). Overall, insights on the decisions by soaring birds of when to depart from a thermal (reported here), how to circle drifted thermals (Harel, Duriez, et al., 2016) and at which speed to glide between thermals (Horvitz et al., 2014) were all made based on fine-resolution data on both the movements of the individual birds, and their immediate environment. This highlights the unique strength of coupling high-resolution data on movements of individual free-ranging animals and their surrounding environment, to elucidate what governs animal decision-making in response to variation in their complex real-life environments.

AUTHORS' CONTRIBUTIONS

R.H. and R.N. designed the study; R.H. performed the fieldwork and analysed the data; R.H. and R.N. wrote the manuscript.

DATA ACCESSIBILITY

The data used in the manuscript are available under the following Movebank (http://www.movebank.org/) project "Soaring flight in Eurasian griffon vultures (HUJ) (data from Harel & Nathan, 2018)" (https://doi.org/10.5441/001.1.46t5141d).

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REFERENCES

Alerstam, T., & Lindström, Å. (1990). Optimal bird migration: The relative importance of time, energy, and safety. In E. Gwinner (Ed.), *Bird migration* (pp. 331–351). Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-642-74542-3

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4.

Bohrer, G., Brandes, D., Mandel, J. T., Bildstein, K. L., Miller, T. A., Lanzone, M., ... Tremblay, J. A. (2012). Estimating updraft velocity components over large spatial scales: Contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters*, 15, 96–103. https://doi.org/10.1111/j.1461-0248.2011.01713.x

Cramp, S. (1985). *The birds of the western palearctic*. Oxford, UK: University Press.

Dale, S., & Slagsvold, T. (1996). Mate choice on multiple cues, decision rules and sampling strategies in female pied flycatchers. *Behaviour*, 133, 903–944. https://doi.org/10.1163/156853996X00305

Fagan, W. F., Gurarie, E., Bewick, S., Howard, A., Cantrell, R. S., & Cosner, C. (2017). Perceptual ranges, information gathering, and foraging success in dynamic landscapes. *The American Naturalist*, 189, 474–489. https://doi.org/10.1086/691099

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., ... Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, 16, 1316–1329. https://doi.org/10.1111/ele.12165

Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C., & McNamara, J. M. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences*, 18, 153–161. https://doi.org/10.1016/j.tics.2013.12.012

Green, R. F. (1984). Stopping rules for optimal foragers. *The American Naturalist*, 123, 30. https://doi.org/10.1086/284184

Harel, R., Duriez, O., Spiegel, O., Fluhr, J., Horvitz, N., Getz, W. M., ... Nathan, R. (2016). Decision-making by a soaring bird: Time, energy and risk considerations at different spatio-temporal scales. *Philosophical transactions of the Royal Society of London B*, 371, 20150397. https://doi.org/10.1098/rstb.2015.0397

Harel, R., Horvitz, N., & Nathan, R. (2016). Adult vultures outperform juveniles in challenging thermal soaring conditions. *Scientific Reports*, 6, 27865. https://doi.org/10.1038/srep27865

Harel, R., & Nathan, R. (2018). Data from: The characteristic time scale of perceived information for decision-making: departure from thermal columns in soaring birds. *Movebank Data Repository*, https://doi.org/10.5441/001/1.46t5141d

Hedenström, A. (2003). *Twenty-three testable predictions about bird flight*. In: P. Berthold, E. Gwinner & E. Sonnenschein (Eds.), *Avian migration* (pp. 563–582). Berlin, Heidelberg: Springer.

Hedenstrom, A., & Alerstam, T. (1995). Optimal flight speed of birds. *Philosophical Transactions of the Royal Society of London B*, 348, 471–487. https://doi.org/10.1098/rstb.1995.0082

Hoover, J. P. (2003). Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology*, 84, 416–430. https://doi.org/10.1890/0012-9658(2003)084[0416:DRFSFI]2.0.CO;2

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? *Ecology Letters*, 17, 670–679. https://doi.org/10.1111/ele.12268

Kacelnik, A., & Krebs, J. R. (1985). Learning to exploit patchily distributed food. In R. M. Sibly, & R. H. Smith (Eds.), *Behavioural ecology: Ecological consequences of adaptive behaviour* (pp. 189–205). Oxford, UK: Blackwell Scientific Publications.

Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Exo, K., Bairlein, F., & Alerstam, T. (2014). When and where does mortality occur in migratory birds ? Direct evidence from long-term satellite tracking of raptors. *Journal of Animal Ecology*, 83, 176–184. https://doi.org/10.1111/1365-2656.12135

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlishaw, G. (2013). How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions. *Journal of Animal Ecology*, 82, 894–902. https://doi.org/10.1111/1365-2656.12089

McNamara, J. M., Green, R. F., & Olsson, O. (2006). Bayes' theorem and its applications in animal behaviour. *Oikos*, 112, 243–251. https://doi.org/10.1111/j.0030-1299.2006.14228.x

Mellone, U., Klaassen, R. H. G., García-Ripollés, C., Limiñana, R., López-López, P., Pavón, D., ... Alerstam, T. (2012). Interspecific comparison of the performance of soaring migrants in relation to morphology, meteorological conditions and migration strategies. *PLoS ONE*, 7, e39833. https://doi.org/10.1371/journal.pone.0039833

Miller, T. A., Brooks, R. P., Lanzone, M. J., Brandes, D., Cooper, J., Tremblay, J. A., ... Katzner, T. E. (2016). Limitations and mechanisms influencing the migratory performance of soaring birds. *Ibis*, 158, 116–134. https://doi.org/10.1111/ibi.12331

Mundy, P., Butchart, D., Ledger, J., & Piper, S. (1992). *The vultures of Africa*. London, UK: Academic Press.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the USA*, 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Nolet, B. A., Klaassen, R. H. G., & Mooij, W. M. (2006). The use of a flexible patch leaving rule under exploitative competition: A field test with swans. *Oikos*, 112, 342–352. https://doi.org/10.1111/j.0030-1299.2006.13460.x

Olsson, O., & Brown, J. S. (2006). The foraging benefits of information and the penalty of ignorance. *Oikos*, 112, 260–273. https://doi.org/10.1111/j.0030-1299.2006.13548.x

Pennycuick, C. J. (1972). Soaring behaviour and performance of some East African birds observed from a motor-glider. *Ibis*, *114*, 178–218.

Pennycuick, C. J., Akesson, S., & Hedenström, A. (2013). Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *Journal of The Royal Society Interface*, *10*, 20130419. https://doi.org/10.1098/rsif.2013.0419

R Core Team (2017). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Reichmann, H. (1978). *Cross-country soaring*, Pacific Palisades, CA, USA: Thomson.

Rus, A. I., Duerr, A. E., Miller, T. A., Belthoff, J. R., & Katzner, T. E. (2017). Counterintuitive roles of experience and weather on migratory performance. *The Auk*, *134*, 485–497. https://doi.org/10.1642/AUK-16-147.1

Sapir, N., Wikelski, M., McCue, M. D., Pinshow, B., & Nathan, R. (2010). Flight modes in migrating european bee-eaters: Heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE*, *5*, e13956. https://doi.org/10.1371/journal.pone.0013956

Shamoun-Baranes, J., Baharad, A., Alpert, P., Berthold, P., Yom-Tov, Y., Dvir, Y., & Leshem, Y. (2003). The effect of wind, season and latitude on the migration speed of white storks *Ciconia ciconia*, along the eastern migration route. *Journal of Avian Biology*, *34*, 97–104. https://doi.org/10.1034/j.1600-048X.2003.03079.x

Shamoun-Baranes, J., Bouten, W., van Loon, E. E., Meijer, C., & Camphuysen, C. J. (2016). Flap or soar? How a flight generalist responds to its aerial environment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 415–422.

Shamoun-baranes, J. A., Leshem, Y., Yom-tov, Y., & Liechti, O. (2003). Differential use of thermal convection by soaring birds over central israel differential use of thermal convection by soaring. *Condor*, *105*, 208–218. https://doi.org/10.1650/0010-5422(2003)105[0208:DUOTCB]2.0.CO;2

Shepard, E. L. C., Lambertucci, S. A., Vallmitjana, D., & Wilson, R. P. (2011). Energy beyond food: Foraging theory informs time spent in thermals by a large soaring bird. *PLoS ONE*, *6*, e27375. https://doi.org/10.1371/journal.pone.0027375

Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A., & Vosper, S. B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist*, *182*, 298–312. https://doi.org/10.1086/671257

Spiegel, O., Harel, R., Centeno-Cuadros, A., Hatzofe, O., Getz, W. M., & Nathan, R. (2015). Moving beyond curve fitting: Using complementary data to assess alternative explanations for long movements of three vulture species. *The American Naturalist*, *185*, E44–E54. https://doi.org/10.1086/679314

Spiegel, O., Harel, R., Getz, W. M., & Nathan, R. (2013). Mixed strategies of griffon vultures' (*Gyps fulvus*) response to food deprivation lead to a hump-shaped movement pattern. *Movement Ecology*, *1*, 5. https://doi.org/10.1186/2051-3933-1-5

Stephens, D. W. (2008). Decision ecology: Foraging and the ecology of animal decision making. *Cognitive, Affective & Behavioral Neuroscience*, *8*, 475–484. https://doi.org/10.3758/CABN.8.4.475

Strandburg-Peshkin, A., Farine, D. R., Crofoot, M. C., & Couzin, I. D. (2017). Habitat structure shapes individual decisions and emergent group structure in collectively moving wild baboons. *eLife*, *6*, e19505.

Taylor, G., Reynolds, K. V., Thomas, A. L. R., & Taylor, G. K. (2016). Soaring energetics and glide performance in a moving atmosphere. *Philosophical transactions of the Royal Society of London B: Biological Sciences*, *371*, 20150398. https://doi.org/10.1098/rstb.2015.0398

Therneau, T. (2012). *coxme: Mixed effects Cox models. R package version 2.2-3*. Vienna: R Foundation for Statistical Computing.

Treep, J., Bohrer, G., Shamoun-Baranes, J., Duriez, O., de Moraes, Prata., Frasson, R., & Bouten, W. (2016). Using high-resolution GPS tracking data of bird flight for meteorological observations. *Bulletin of the American Meteorological Society*, *97*, 951–961. https://doi.org/10.1175/BAMS-D-14-00234.1

Vansteelant, W. M. G., Bouten, W., Klaassen, R. H. G., Koks, B. J., Schlaich, A. E., van Diermen, J., … Shamoun-Baranes, J. (2015). Regional and seasonal flight speeds of soaring migrants and the role of weather conditions at hourly and daily scales. *Journal of Avian Biology*, *46*, 25–39.

Vansteelant, W. M., Shamoun-Baranes, J., McLaren, J., van Diermen, J., & Bouten, W. (2017). Soaring across continents: Decision-making of a soaring migrant under changing atmospheric conditions along an entire flyway. *Journal of Avian Biology*, *48*, 887–896. https://doi.org/10.1111/jav.01298

Videler, J. J. (2006). *Avian flight*. Oxford, UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199299928.001.0001

Wajnberg, E., Fauvergue, X., & Pons, O. (2000). Patch leaving decision rules and the Marginal Value Theorem: An experimental analysis and a simulation model. *Behavioral Ecology*, *11*, 577–586. https://doi.org/10.1093/beheco/11.6.577

Weimerskirch, H., Bishop, C., Jeanniard-du-Dot, T., Prudor, A., & Sachs, G. (2016). Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science*, *353*, 74–78. https://doi.org/10.1126/science.aaf4374

Weinzierl, R., Bohrer, G., Kranstauber, B., Fiedler, W., Wikelski, M., & Flack, A. (2016). Wind estimation based on thermal soaring of birds. *Ecology and Evolution*, *6*, 8706–8718. https://doi.org/10.1002/ece3.2585

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