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Soaring across continents: decision-making of a soaring migrant under changing atmospheric conditions along an entire flyway

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Thermal soaring birds reduce flight-energy costs by alternately gaining altitude in thermals and gliding across the earth's surface. To find out how soaring migrants adjust their flight behaviour to dynamic atmospheric conditions across entire migration routes, we combined optimal soaring migration theory with high-resolution GPS tracking data of migrating honey buzzards *Pernis apivorus* and wind data from a global numerical atmospheric model.

We compared measurements of gliding air speeds to predictions based on two distinct behavioural benchmarks for thermal soaring flight. The first being a time-optimal strategy whereby birds alter their gliding air speeds as a function of climb rates to maximize cross-country air speed over a full climb–glide cycle (V_{opt}). The second a risk-averse energy-efficient strategy at which birds alter their gliding air speed in response to tailwinds/headwinds to maximize the distance travelled in the intended direction during each glide phase (V_{bgw}).

Honey buzzards were gliding on average 2.05 ms^{-1} slower than V_{opt} and 3.42 ms^{-1} faster than V_{bgw} while they increased air speeds with climb rates and reduced air speeds in tailwinds. They adopted flexible flight strategies gliding mostly near V_{bgw} under poor soaring conditions and closer to V_{opt} in good soaring conditions.

Honey buzzards most adopted a time-optimal strategy when crossing the Sahara, and at the onset of spring migration, where and when they met with the best soaring conditions. The buzzards nevertheless glided slower than V_{opt} during most of their journeys, probably taking time to navigate, orientate and locate suitable thermals, especially in areas with poor thermal convection.

Linking novel tracking techniques with optimal migration models clarifies the way birds balance different tradeoffs during migration.

List of symbols and abbreviations

β Angle between heading and track direction over full climb–glide cycle. V_a Gliding air speed. V_{ac} Horizontal air speed during the climb phase. V_{bg} Theoretical best-gliding air speed for maximizing gliding range relative to the air. V_{bgw} Theoretical best-gliding air speed for maximizing gliding range relative to the ground. V_c Climb rate. V_{cc} Cross-country speed relative to the air. V_g Gliding ground speed. V_h Ground speed during the climb phase (mostly due to advection by wind). V_{ms} Theoretical minimum-sink speed. V_{opt} Theoretical optimal air speed for maximizing V_{cc} . V_s Sink rate. V_{xc} Cross-country speed relative to the ground. TEA Thermal exit altitude. T_c Time spent climbing. T_{cc} Time spent across entire climb–glide cycle. T_g Time spent gliding. W_{sg} Sidewind component relative to glide direction. W_{Sxc} Sidewind component relative to track direction across entire climb–glide cycle. W_{Tg} Tailwind component relative to glide direction. W_{Txc} Tailwind component relative to track direction across entire climb–glide cycle.

Migrant birds face highly variable weather conditions during their seasonal journeys and use various strategies to reduce the energetic cost and time needed to complete their migration (Alerstam 1991, 2011). Soaring birds generally avoid

active flapping flight by gaining altitude in thermals on stretched wings, after which they glide across the landscape, thus reducing the amount of energy spent (Pennycuik 1978, 2008, Kerlinger 1989, Bildstein 2006) and extending their migratory range (Watanabe 2016). Consequently, variability in both soaring and wind conditions determine much of the variation in the hourly travel speeds and daily travel distances of soaring migrants (Shamoun-Baranes et al. 2003a, Mandel et al. 2008, Mellone et al. 2012, Vansteelant et al. 2015).

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To cope with highly dynamic atmospheric conditions along their journeys, soaring migrants may adopt flexible flight modes (Lanzone et al. 2012, Duerr et al. 2014). As yet it is not known how thermal-soaring birds adjust their objectives while gliding between thermals in changing weather conditions throughout their cross-continental journeys. Using recent improvements in tracking technology (Bouten et al. 2013, Kays et al. 2015) we were able to sample fine-scale flight behaviour of a soaring migrant across an entire migration cycle. By comparing measured gliding air speeds with predictions from two optimal soaring migration models we aim to determine how soaring migrants adjust their fine-scale soaring behaviour to changing atmospheric conditions en route.

Optimal soaring migration theory

Optimal soaring migration theory is a framework used to calculate benchmark behaviours against which the flight behaviour of soaring migrants can be compared (Hedenström 1993, 1997, Spaar and Bruderer 1997, Pennycuick 2008). A soaring bird gains potential energy by circling upward in a thermal, and converts this potential energy into kinetic energy by gliding between thermals to make fast progress across the ground (Fig. 1A). The horizontal gliding air speed (V_a) increases with sink rate (V_s), but sinking fast results in short glides decreasing overall progress relative to still air. The relationship between sink rate and gliding air speed can be solved graphically as the 'glide polar' (Fig. 1B–C) to derive optimal soaring strategies according to various criteria. The glide polar depends on drag forces acting on a bird (Pennycuick 1968, 2008, Tucker and Parrott 1970, Tobalske 2007), that in turn depend on the bird's mass, as well as wing area and wing shape, both adjustable to control air speeds (Parrott 1970, Tucker and Parrott 1970, Pennycuick 1978, 2008, Tucker and Heine 1990).

The time-minimization strategy

To model soaring flight, a simplified soaring trajectory in windless conditions is used, in which a bird glides between discrete thermals, gliding down to the same altitude at which it started climbing (Fig. 1A). In a time-minimizing strategy the cross-country air speed (V_{cc}) and cross-country ground speed (V_{xc}), the average speed relative to the air or the ground over a full climb–glide cycle, is maximized (Hedenström 1993, 1997, Alerstam and Hedenström 1998, Pennycuick 2008). V_{opt} is the gliding air speed at which V_{cc} is maximal. V_{cc} can be calculated in terms of the time spent climbing (T_c) and gliding (T_g) as follows:

$$V_{cc} = V_a \times \frac{T_g}{T_g + T_c} \quad (1)$$

If we assume that the altitude over which a bird sinks during the glide (Δh) is the same as the altitude over which it climbed in the preceding thermal (Fig. 1A), then T_g and T_c can be solved in terms of Δh and the vertical speed in the glide (V_s) and climb phase (V_c) respectively:

$$\Delta h = T_g \times V_s = T_c \times V_c \quad (2)$$

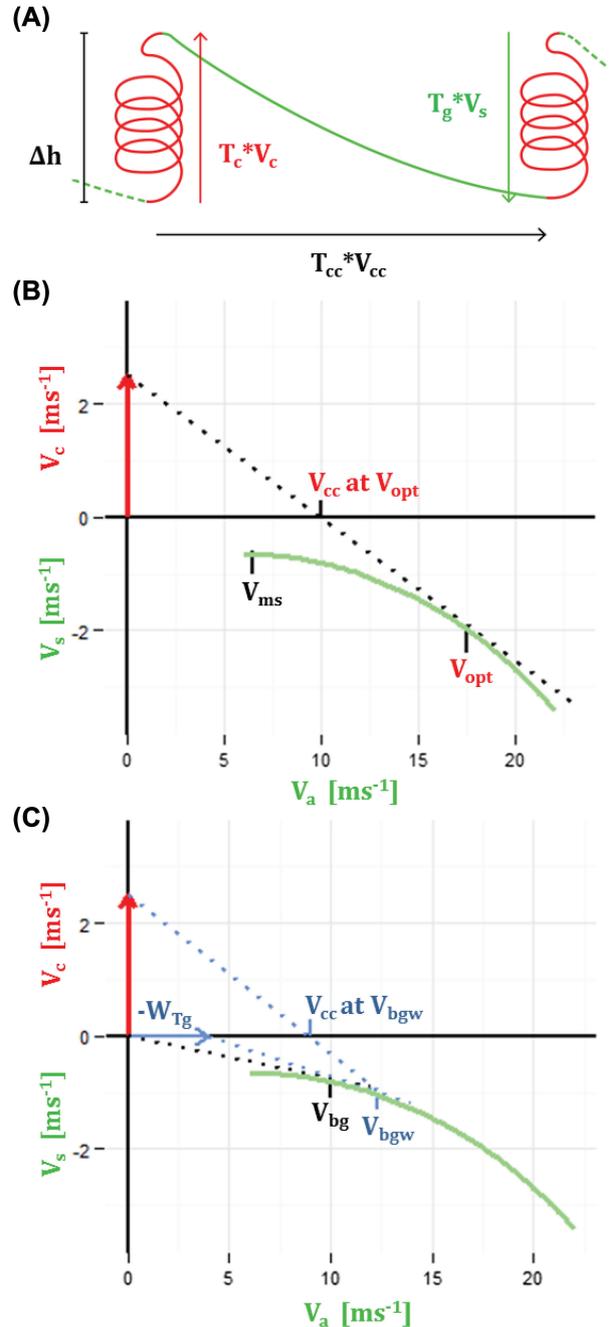


Figure 1. Optimal soaring migration models. (A) We assumed an idealized soaring trajectory in order to predict optimal gliding air speeds. (B) For any given bird, the glide polar (green) depicts the relationship between V_a and V_s which determines how fast a bird should glide depending on its objective. While the rate at which altitude is lost is minimal at minimum sink speed (V_{ms}) migrants should glide faster than V_{ms} to ensure efficient travel. The optimal air speed V_{opt} to maximize V_{cc} as a function of V_c is found by drawing a tangent from the observed climb rate in a thermal on the y-axis ($0, V_c$). The point where the tangent crosses the x-ordinate is the corresponding V_{cc} . (C) The best-gliding air speed V_{bg} maximizes gliding range in windless conditions and is found on the tangent from the origin of the coordinate system ($0, 0$). We extended this model to maximize glide range relative to the ground in head-/tailwinds by drawing a tangent from $(-W_{Tg}, 0)$ instead. The example shows V_{bgw} for gliding in a headwind.

Thus we can substitute T_g and T_c in Eq. 1 to predict V_{opt} , the gliding air speed at which a bird reaches maximal V_{cc} , for a given V_c (graphical solution in Fig. 1B):

$$V_{cc} = V_a \times \frac{V_c}{V_s + V_c} \quad (3)$$

The risk-avoidance strategy

An alternative soaring strategy is to achieve maximal range relative to the air during the glide phase, that may well be necessary to avoid the need for flapping flight when thermals are too far apart to reach within a single glide at a “time-minimizing” air speed V_{opt} (Pennycuik 2008). To reach maximal range between thermals in windless conditions, a bird must glide at its best-gliding air speed (V_{bg}), the air speed to minimize its glide ratio (graphical solution Fig. 1C):

$$GR = \frac{V_s}{V_a} \quad (4)$$

While many soaring migrants increase their gliding air speeds and cross-country air speeds with improving soaring conditions, as expected for V_{opt} (Kerlinger et al. 1985, Bruderer et al. 1994, Spaar 1997), others, such as the white stork *Ciconia ciconia*, apparently do not (Liechti et al. 1996). Comparative analysis of various species suggest soaring migrants usually do not reach V_{opt} in a glide (Spaar and Bruderer 1996, 1997, Horvitz et al. 2014). In fact, out of 12 species of soaring migrants tracked by radar while migrating over Israel, none were gliding as fast as V_{opt} , and gradually reduced air speeds toward V_{bg} under deteriorating soaring conditions, probably to avoid the risk of not reaching another thermal between glides (Horvitz et al. 2014). The most risk-averse species were those with the highest wing loadings, i.e. those for which energetic costs of flapping flight are highest (Horvitz et al. 2014). However, a strictly risk-averse strategy is perhaps surprising for soaring migrants travelling over Israel given that thermals tend to be strong and abundant there (Leshem and Yom-Tov 1996, Spaar et al. 2000, Shamoun-Baranes et al. 2003c).

The importance of wind

Wind conditions determine much of the variation in the ground speed of soaring migrants (Shamoun-Baranes et al. 2003a, Mandel et al. 2008, Mellone et al. 2012, Vansteelandt et al. 2015), making wind an important selective agent in the evolution of soaring flight behaviour (Alerstam 1979a, Richardson 1990, Kranstauber et al. 2015). There is evidence that some soaring migrants tend to reduce their gliding air speeds in tailwinds (Spaar and Bruderer 1996, 1997, Malmiga et al. 2015). However, this behaviour cannot be explained from time-optimal flight strategy because a bird will maximize cross-country air speed (V_{cc}) as well as cross-country ground speed (V_{xc}) in any wind conditions by gliding at V_{opt} (Alerstam and Hedenström 1998).

Adjustments in gliding air speed because of wind conditions only make sense if birds aim to maximize the distance they can cover relative to the ground during a glide, e.g. after leaving a weak and shallow thermal. Glider pilots will increase their air speed in headwind, and decrease it in tailwind, by about half of the headwind/tailwind component,

if they want to maximize their gliding range (Rogers 1999). Similarly, griffon vultures *Gyps fulvus* were recently found to adjust prioritization of energy and time-efficient behaviours depending on local wind conditions during foraging flights (Harel et al. 2016).

Integrating headwinds and tailwinds in risk-averse soaring migration models

In order to incorporate wind into optimal migration models we need to make certain assumptions about orientation behaviour. Here we introduce a simple model assuming a bird is fully drifting with the wind (i.e. ignoring side winds) or maximizing its progress along its heading. To account for wind along any heading we define the best-gliding air speed (V_{bgw}) as the gliding air speed that minimizes the ratio of sink to ground speed along that heading (Fig. 1C):

$$f(V_a) = \frac{V_s}{V_a + W_{Tg}} \quad (5)$$

where W_{Tg} is the tailwind/headwind relative to the bird’s gliding heading.

Combining optimality theory with high-resolution GPS tracking

We measured soaring flight behaviour of five European honey buzzards *Pernis apivorus* across an entire migration cycle and compare their gliding air speeds with predictions for two behavioural benchmarks derived from optimal soaring migration models:

- a time-minimizing strategy for cross-country soaring, whereby birds adjust gliding air speed to climb rates in thermals (V_{opt}) to maximize cross-country air speed and ground speed
- a risk-averse strategy for gliding, whereby birds adjust gliding air speed to headwinds and tailwinds, gliding at air speeds (V_{bgw}) that maximize their gliding range relative to the ground.

When considering flight across the entire migration journey, we expect honey buzzards to glide at air speeds approaching V_{opt} under good soaring conditions and in weak winds while we expect gliding air speeds to approach V_{bgw} under poor soaring conditions and strong winds. On average we expect to find gliding air speeds intermediate to V_{opt} and V_{bgw} and we use the risk-averse flight index (RAFI, Horvitz et al. 2014) to quantify how airspeed compared to V_{opt} and V_{bgw} in every glide:

$$RAFI = \frac{V_{opt} - V_a}{V_{opt} - V_{bgw}} \quad (6)$$

V_{opt} is always greater than V_{bg} and so in the formulation of Horvitz et al. (2014) negative values of RAFI only occur when migrants increase V_a beyond V_{opt} , and RAFI exceeds 1 only if birds fly at V_a lower than V_{bg} . However, V_{opt} can theoretically be lower than V_{bgw} when birds encounter both weak thermals and strong headwinds. Consequently, in our formulation, RAFI may become negative if $V_a < V_{opt} < V_{bgw}$ and RAFI may exceed values of 1 if $V_a > V_{bgw} > V_{opt}$. However, we expect that in reality birds rarely travel into a strong headwind when thermals are weak (either by changing

travel direction or interrupting travel) and so V_{opt} should be greater than V_{bgw} in most cases. Consequently, we expect the interpretation of RAFI is comparable in our study as in the study of Horvitz et al. (2014), with $RAFI < 0$ indicating that birds glide at $V_a > V_{opt} > V_{bgw}$ and $RAFI > 1$ indicating that birds glide at $V_a < V_{bgw} < V_{opt}$. We expect migrating soaring birds will approach V_{opt} in good soaring conditions while they should reduce their gliding air speed, approaching V_{bgw} in poor soaring conditions. Such behavioural flexibility should enable them to cope with heterogeneous weather conditions encountered within an entire flyway. We thus also explore geographical and seasonal patterns in RAFI in relation to geographical and seasonal variability in thermal exit altitudes (TEA) as a measure of soaring conditions. In doing so, we aim to improve our understanding of soaring migration ecology and hope to stimulate the integration of optimality theory in animal movement research.

Material and methods

Study species

The honey buzzard that we tracked breed in the Netherlands and migrate along the east-Atlantic flyway, using the Strait of Gibraltar as a strategic passage point in both autumn and spring (Vansteelant et al. 2015). Adults leave the breeding grounds by mid or late August to arrive at the wintering grounds in September–October (Hake et al. 2003, Ferguson-Lees and Christie 2006, Vansteelant et al. unpubl.) and depart from their wintering grounds in tropical Africa starting early April to arrive at their breeding grounds by early-mid May.

Because honey buzzards have a relatively low wing loading compared to many other soaring migrants they can soar in relatively weak thermals shortly after sunrise until late in the evening (Bruderer et al. 1994, Leshem and Yom-Tov 1996, Vansteelant et al. 2014). This low wing loading also permits honey buzzards to use a larger proportion of the boundary layer depth than larger and heavier species (Shamoun-Baranes et al. 2003b) and our data shows that across entire migratory journeys honey buzzards spend at least 93% of their flight time soaring (Bouten unpubl. accelerometer data). As honey buzzards keep soaring under a wide range of weather conditions, they represent an excellent species with which to study the role of wind and soaring conditions for optimal soaring migration.

The GPS experiment

We developed an experiment for five honey buzzards that we fitted with highly flexible and remotely programmable GPS-loggers (<www.uva-bits.nl>; Bouten et al. 2013). A detailed description of our trapping and handling procedures are provided in (Vansteelant et al. 2015). Before honey buzzards departed from the breeding grounds in August 2012, we remotely uploaded a measurement scheme for recording 3D GPS locations at 10 second resolution between 10:00–10:30 UTC and again between 12:00–12:30 UTC for each day a bird spent between latitude 52N and 10N. From previous studies, we expected that 10 s resolution

would be adequate to resolve climbs and glides while not overloading logger memory, nor the download capacity of the data retrieving system. Data were downloaded through a relay network with a remotely accessible base station in the breeding territories. We retrieved 360 half hour segments of high-resolution data (Fig. 2A).

Assuming birds use discrete thermals (Pennycuik 1998a, 2008) their cross-country flight can be split into a series of climb–glide cycles. First we calculated the distance, altitude difference and duration between consecutive GPS locations to determine ground speeds and vertical speeds. We then calculated the running average of a bird's vertical speed from two fixes before (ca 20 s) until two fixes after (ca 20 s) each location. Locations where the running average vertical speed switched from positive to negative were taken as the starting point of a new gliding bout, and vice versa for every climb (Fig. 2B). We paired each climbing phase with its consecutive gliding phase to obtain 1282 climb–glide cycles of which 1178 cycles were recorded completely (Fig. 2A).

We removed 21 climb–glide cycles during which birds travelled less than 2000 m between the start and end of the cycle. These cycles consisted of highly tortuous movements across complex terrain, suggesting honey buzzards rather responded to surface-conditions than weather. In addition, visual inspection of altitudinal profiles revealed that some of the high-resolution segments recorded were at constant altitudes that likely consisted of flapping flight instead of soaring flight. These segments mainly occurred in strong headwinds above tropical rainforest in western Africa and flight altitude usually did not exceed 250 m above the ground during these flights. Because we are only interested in thermal soaring flight, we removed all cycles where birds did not exceed 250 m (151 of 1157 cycles), as we expected these altitudes to be too low to support thermal soaring (Shamoun-Baranes et al. 2003b).

We calculated climb rate (V_c) between the first and the last location of each climb phase and analogously track direction, sink rate (V_s) and ground speed (V_g) during each glide. We finally calculated cross-country speeds relative to the ground (V_{xc}) between the start of the climb phase and the end of a glide.

Interpolating wind conditions and calculating air speeds

We obtained wind estimates from the 925 hPa pressure level in the European Centre for Medium-range Weather Forecast (ECMWF) HRES model (ECMWF 2016), corresponding to an average flight altitude of ca 700 m above mean sea level (Supplementary material Appendix 1 Table A1). ECMWF forecasts provide wind vectors at a resolution of three hours and 0.25 degrees and thus resolve mesoscale atmospheric processes. Even though honey buzzards constantly change altitude during soaring and gliding bouts, within the well-mixed boundary layer utilized by honey buzzards, wind speed and direction do not vary much with altitude (Stull 1988). Due to the spatial scope of our study and the properties of a mixed boundary layer we do not expect differences in the altitude and resolution of our wind data compared to tracking data to cause an asymmetric bias with actual wind conditions.

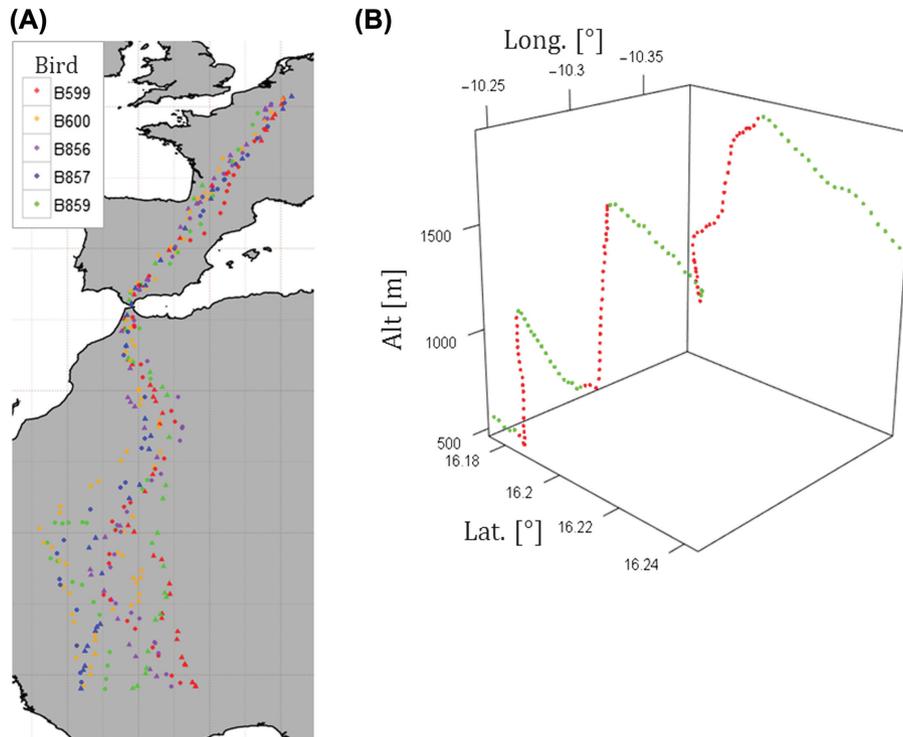


Figure 2. Capturing soaring behaviour of honey buzzards with high-resolution GPS loggers. (A) Location of half-hour segments of high resolution measurements (measurement frequency 10 s) of soaring flight taken twice a day between 52N and 10N during autumn 2012 (triangles) and spring 2013 (circles) for each individual (colour code). (B) Each half-hour segment of GPS-observations was divided into climb (red) and glide phases (green). The half hour segment depicted here yielded two uninterrupted climbing–gliding cycles for our analyses.

Within each full climbing and gliding cycle, wind vectors were linearly interpolated in space and time to the starting point of each climbing and gliding phase. We then used vector trigonometry to determine the air speeds of honey buzzards while gliding (V_a) and across full climbing–gliding cycles (V_c) from the corresponding ground speeds, track directions and local wind vectors (Liechti and Bruderer 1998).

We used linear regression models to test for possible correlations between wind conditions and soaring conditions since thermals tend to lose vertical velocity in strong winds (Stull 1988). We also tested for correlation between thermal exit altitudes (TEA) and climb rates V_c (Shamoun-Baranes et al. 2003b).

Modelling time-optimal and risk-averse soaring strategies

We implemented aerodynamic equations (Pennycuick 2008) in R (ver. 2.15.0; <www.r-project.org>) for a theoretical honey buzzard with a mass of 1 kg, a wingspan of 1.3 m, a wing surface area of 0.26 m² (measurements from <www.sempach.ch>) and a body drag coefficient of 0.25 [-] flying at an average altitude of 700 m (Supplementary material Appendix 1 Fig. A1), corresponding to an air density of 1.15 kg m⁻³. To calibrate the model we used standard settings, using a planform slope of 1 to assume linear decrease of wing area with wingspan as birds flex their wings while increasing air speed, and a wingspan reduction constant of 5. We compared the glide polar and concomitant V_{opt} with

those produced by the program ‘Flight’ (ver. 1.23) using the same model parameterization and found no differences (Pennycuick 2008).

Comparing theoretical and measured responses to climb rates and tailwinds

Our main purpose was to evaluate to what extent the birds adjusted gliding airspeeds in relation to V_c and W_{Tg} and how this compared with the predictions according to V_{opt} and V_{bgw} , respectively. In order to allow for non-linear relationships that were not defined a priori, we used 2nd order loess regression models (Cleveland and Devlin 1988) that are able to resolve more complex behavioural dynamics than simple linear models.

Seasonal and regional flexibility in risk-aversion and soaring conditions

The risk-averse flight index (RAFI) compares the measured gliding air speeds with V_{opt} and V_{bgw} to yield a measure of risk-aversion. $RAFI = 0$ when $V_a = V_{opt}$ and $RAFI = 1$ when $V_a = V_{bgw}$. Assuming that V_{opt} is always greater than V_{bgw} , we expect that in most cases $0 < RAFI < 1$, that $RAFI < 0$ if birds glide at $V_a > V_{opt} > V_{bgw}$ and that $RAFI > 1$ if birds glide at $V_a < V_{bgw} < V_{opt}$. As explained in the introduction, other interpretations are possible if V_{opt} is lower than V_{bgw} which may be the case when honey buzzards encounter weak thermals and strong headwinds. However, we expect honey buzzards usually avoid flying into headwinds in weak

thermals, either by adjusting their heading or interrupting travel. We quantify risk-aversion along the entire migration cycle using an adapted risk-averse flight index (RAFI, Horvitz et al. 2014, Harel et al. 2016), using V_{bgw} instead of V_{bg} as the benchmark for risk-aversion. We then use loess regression models to explore how RAFI and thermal exit altitudes (TEA) vary with latitude during autumn and spring.

Sensitivity analysis

It is important to consider that the body drag coefficient and several other dimensionless coefficients for describing theoretical relationships between air speed and drag forces in flight mechanical theory are estimated with considerable uncertainty. These coefficients could be highly influential for predictions of gliding performance (Pennycuik 2008). For example, the body mass of honey buzzards is likely to change substantially throughout the year as they fatten up before the onset of migration and progressively deplete their fat stores during travel (Glutz von Blotzheim et al. 1971). Consequently, we conducted a sensitivity analysis for the most influential and poorly calibrated variables in our reference model (Supplementary material Appendix 2 Fig. A1).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.bp70s>> (Vansteelant et al. 2017).

Results

We identified 1006 climb–glide cycles from honey buzzards’ vertical speeds that were used in subsequent analysis (Fig. 2A–B). The number of climb–glide cycles, the weather variables and the flight parameters are summarized for each individual and across the entire dataset in Supplementary material Appendix 1 Table A1 and Fig. A1 (see also ‘List of symbols and abbreviations’).

Thermal exit altitudes increased strongly with climb rates in thermals (thermal exit altitude = $247.81 + 304.55 \times V_c$; $p < 2 \times 10^{-16}$, $R^2 = 0.28$). Horizontal wind components were very weakly correlated with climb rates and thermal exit altitudes ($R^2 < 0.02$ in all cases) and thus were unlikely to bias our analyses across the entire dataset (Supplementary material Appendix 1 Table A2).

Measured versus predicted air speeds

The predicted minimum sink speed (V_{ms}) was 6.50 ms^{-1} and the best-gliding air speed in windless conditions (V_{bg} , i.e. V_{bgw} at $W_{Tg} = 0 \text{ ms}^{-1}$) was 10.02 ms^{-1} (Fig. 1B–C). Measured gliding air speeds ($\bar{V}_a = 13.60 \text{ ms}^{-1}$) varied between 1.68 ms^{-1} and 27.07 ms^{-1} (Supplementary material Appendix 1 Fig. A1), with values lower than the minimum sink speed V_{ms} on 20 out of 1006 occasions. Theoretically, such low air speeds are presumed not to occur and they are likely to be caused by overestimating wind speeds due to inaccuracies in the global weather model. The highest air speeds were within the range of V_a previously recorded for this species

(7–27 ms^{-1} , Bruderer and Boldt 2001). Consequently, we maintained air speeds below V_{ms} to avoid an asymmetric bias in our data.

Predicted V_{opt} varied between 10.12 ms^{-1} and 21.61 ms^{-1} , $\bar{V}_{opt} = 15.61 \text{ ms}^{-1}$ (Fig. 3A). Birds were gliding on average 2.05 ms^{-1} slower than V_{opt} (Fig. 3A, Welch t-test: $p < 2.2 \times 10^{-16}$). The loess regression curves of measured V_a and predicted V_{opt} as a function of climb rates (Fig. 3A) run parallel to each other, showing that honey buzzards increased V_a with V_c at a similar rate as predicted by V_{opt} . Predicted V_{bgw} varied from 7.90 to 21.70 ms^{-1} , $\bar{V}_{bgw} = 10.19 \text{ ms}^{-1}$ (Fig. 3B). Birds were gliding on average 3.42 ms^{-1} faster than at V_{bgw} (Fig. 3C, Welch t-test: $p < 2.2 \times 10^{-16}$). As expected, V_a decreased with W_{Tg} , but linearly instead of asymptotically (Fig. 3B).

Seasonal and regional flexibility in migratory flight strategies

V_{bgw} rarely exceeded V_{opt} (51 cases, $< 1\%$ of all data), including 4 out of 269 cases where $RAFI < 0$ and 18 out of 205 cases where $RAFI > 1$. This confirms that we can interpret RAFI-values analogously to Horvitz et al. (2014), with $RAFI < 0$ indicating that birds were gliding

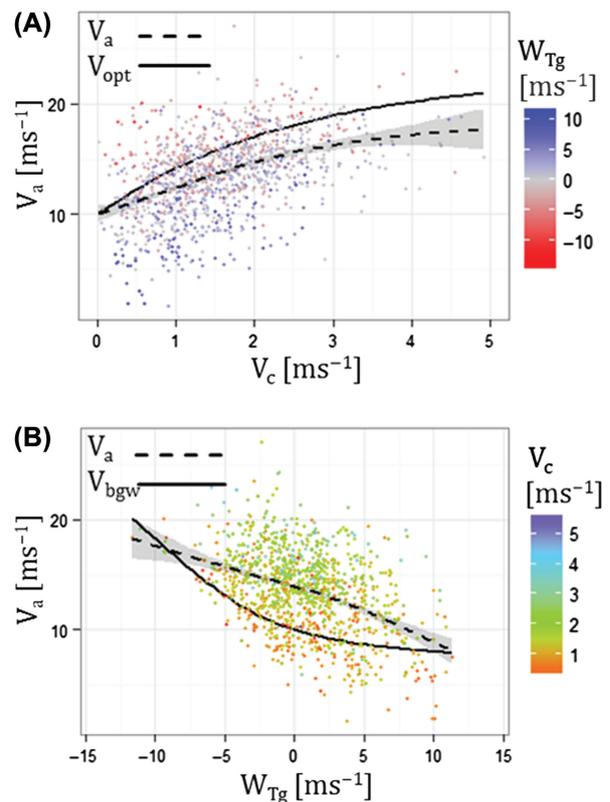


Figure 3. Comparison of measured and predicted optimal gliding air speeds of honey buzzards under variable conditions. (A) A 2nd order loess regression model for measured V_a (dashed line) and predicted V_{opt} (solid line) as a function of climb rates (V_c). Measurements are colour coded depending on the head/tailwinds encountered while gliding (W_{Tg}). (B) A 2nd order loess regression model for the measured V_a (dashed line) and predicted V_{bgw} (solid line) as a function of W_{Tg} . Measured V_a are colour coded depending on the climb rate in the preceding thermal (V_c).

at $V_a > V_{opt} > V_{bgw}$, and $RAFI > 1$ indicating that birds were gliding at $V_a < V_{bgw} < V_{opt}$. RAFI values nonetheless included many outliers. We therefore confined our analysis of seasonal and regional flexibility in RAFI to the core 90% of our observations ($-0.72 < RAFI < 1.76$). Linear regression revealed that across the entire dataset RAFI was significantly negatively related to TEA ($RAFI = 0.54 - 0.00023 \times TEA$, $P_{intercept} = 8.23 \times 10^{-12}$, $P_{slope} = 8.23 \times 10^{-12}$) although this model only explained 5% of variability in RAFI (Supplementary material Appendix 1 Fig. A2).

The loess regression models indicate that RAFI and TEA vary substantially across latitudes, and that these geographical patterns differed between seasons (Fig. 4). Honey buzzards compromised between time-optimal and risk-averse migration strategies throughout the entire autumn migration. In autumn, honey buzzards encountered the best soaring conditions over the Mediterranean and northern Sahara (latitude $25^\circ N - 30^\circ N$) where they also flew at speeds closest to V_{opt} (Fig. 4, TEA). During spring migration, the birds gradually decreased their gliding air speeds from initially near V_{opt} to adopting a more risk-averse strategy when closer to their breeding grounds. Additionally, the birds increased gliding air speeds toward V_{opt} whilst crossing the Sahara (yellow band, Fig. 4) in accordance with peak availability of good soaring conditions (high TEA) (latitude $35^\circ N$).

Sensitivity analysis

Full explanation and results of the sensitivity analysis with respect to uncertainties in the parameterization of the optimal soaring migration model are reported in Supplementary material Appendix 2.

Discussion

Consistent with a time-optimal soaring migration strategy and previous radar-tracking studies of soaring migrants (Kerlinger and Gauthreaux 1985, Kerlinger 1989, Spaar and Bruderer 1997, Spaar 1997), we found that honey buzzards

increased their gliding air speeds with higher climb rates in thermals. However, the birds were gliding slower than V_{opt} during most of their journey and reacted to headwinds and tailwinds as expected from a risk-averse migration strategy that maximizes range relative to the ground between thermals (V_{bgw}). Our sensitivity analyses revealed that the honey buzzards would need to have a much lower body mass and higher body drag coefficient than we consider to be realistic in order for the measured air speeds to be optimal for travel time-minimization. While the low spatial and temporal resolution of wind data compared to tracking data increases the noise in our calculations, it is unlikely that this causes asymmetric bias in calculated air speeds. Therefore, our study shows that honey buzzards glide at air speeds slower than V_{opt} , and that they do this in order to reduce the risk of excessive energy consumption under poor soaring conditions (Horvitz et al. 2014). This hypothesis is further supported by our finding that honey buzzards glide near V_{bgw} in areas where they leave thermals at low altitude, whereas they glide closer to V_{opt} in fair soaring conditions (Horvitz et al. 2014).

Several other factors may mitigate the need for soaring birds to glide at time-optimal air speeds. For example, optimal theory assumes that birds enter and exit a climb–glide cycle at the same altitude. However, by exploiting the best thermals (Leshem and Yom-Tov 1996, Pennycuik 1998a) and the strongest lift within those thermals (Shamoun-Baranes et al. 2003b) they can achieve greater migration speed in other ways than by gliding at V_{opt} . Migrant birds can also reduce travel time by adjusting orientation behaviour in relation to wind (Alerstam 2011, McLaren et al. 2014). Migration routes of soaring birds are generally longer than those of flapping landbirds (Watanabe 2016), sometimes further than what is theoretically feasible in windless conditions (Smith et al. 1986), suggesting they depend on wind to conserve energy as well. Soaring birds frequently adjust orientation behaviour relative to winds encountered en route (Klaassen et al. 2011, Limiñana et al. 2013, Vidal-Mateo et al. 2016) and honey buzzards do so making use of global aerial flyways that provide more wind assistance than they could harness elsewhere (Vansteelant et al. 2016, Kranstauber et al. 2015). Much of the remaining variability in gliding air speeds is likely to be resolved by integrating orientation behaviours in future optimality models (Alerstam 1979b, Liechti and Bruderer 1998, Liechti 2006). In addition, gliding slow may help birds gain time to keep track of leading lines (Mueller and Berger 1967), to locate good thermals (Van Loon et al. 2011, Lanzone et al. 2012, Duerr et al. 2014) and roost-sites (Leshem and Yom-Tov 1998) as well as to look for experienced conspecifics to guide the way (Hake et al. 2003, Chernetsov et al. 2004, Mellone et al. 2011, Van Loon et al. 2011). On the whole, soaring migrants probably do not gain much benefit from ‘racing against the clock’ all the time, as long as they leave on time and they don’t get lost or delayed by unusually bad weather en route (Thorup et al. 2006, Duerr et al. 2012). Consequently, honey buzzards are likely to glide at fast, time-optimal air speeds only in those areas where the best soaring conditions occur.

Contrary to many other long-distance migrants honey buzzards do not speed up migration by increasing air speed when approaching the breeding grounds (Nilsson et al. 2013). This can be explained by the fact they experience relatively

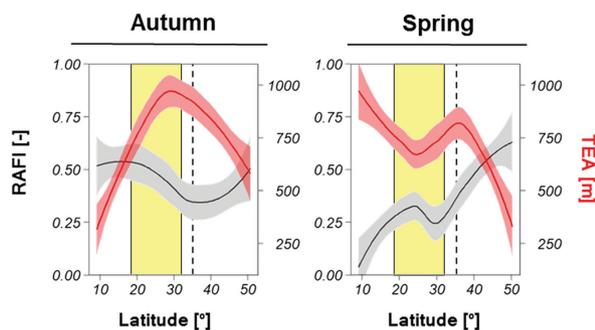


Figure 4. Seasonal and latitudinal patterns in risk aversion by honey buzzards and the soaring conditions en route. Each graph shows a 2nd order loess regression model (span = 0.75, $y \sim x^2$) for RAFI (grey curves) and for thermal exit altitudes (TEA, red curves). Shaded areas around the curves indicate SE at each point along the curve. For reference we indicate the position of the Sahara (yellow box) and the Strait of Gibraltar (dashed line). Note that birds move from north to south (right to left) in autumn and from south to north (left to right) in spring.

poor soaring conditions in this part of their migration cycle. Moreover, honey buzzards still achieve moderate to high ground speeds over Europe in spring due to the occurrence of favourable tailwinds (Kemp et al. 2010, Vansteelant et al. 2015). However, honey buzzards, especially females, also lengthen travel time by making stopovers in Europe during spring, even when the weather is favourable for migration (unpubl. data). This suggests that in addition to weather condition, sex-specific internal factors also influence the inclination of honey buzzards to migrate slowly in the last leg of their spring migration. We think that the slow spring migrations of honey buzzards are indicative of a capital breeding strategy. Even if these migrants can produce more chicks by arriving early, in capital-breeding species females must arrive with sufficient energy reserves to produce eggs shortly upon arrival (Nolet 2006, Kölzsch et al. 2016).

Implications for movement ecology

Our study suggests that the nature of birds' responses to weather conditions and other environmental factors changes along their route (Tøttrup et al. 2008, Klaassen et al. 2011). Thus a combination of weather conditions experienced en route and variable response to those conditions are the predominant behavioural adaptations that drive regional and seasonal differences in the flight speeds of soaring migrants (Vansteelant et al. 2015). Intrinsic motivation to minimize travel time or energy expenditure may vary between seasons causing different response to weather conditions and resulting migration speed (Nilsson et al. 2013, Kölzsch et al. 2016).

Atmospheric conditions also govern decision-making of soaring birds during foraging flights (Shepard et al. 2011, Harel et al. 2016). We ultimately expect larger and heavier species, whose movement capacity (sensu Nathan et al. 2008) depends on the availability of thermals, to be more prone to risk-averse flight across multiple scales of movement (Horvitz et al. 2014). On-going rapid advances in avian tracking are paving the way for comparative studies between different species of soaring birds, as well as many other migrants (Bridge et al. 2011, Bouten et al. 2013, Dodge et al. 2013). For example, high-resolution tracking has revealed that flapping birds such as lesser black-backed gulls *Larus fuscus* fly under maximum-range speed during long-distance flights, despite showing an adaptive response to wind (McLaren et al. 2016). Future studies must make use of emerging opportunities to unify movement ecology research across taxa with different flight modes. Using the concept of 'energy height' researchers can compare energy acquisition and expenditure of birds irrespective of physiology and flight mode (Pennycuik 2003). Using the concept of 'energy landscapes' it is also possible to quantify availability of both biotic (i.e. food) and abiotic (i.e. flows) resources (Shepard et al. 2013) that are used disproportionately by species with different flight modes. There is indeed great potential for the integration of optimality theory and comparative tracking studies to generate new insights into the evolution of avian movement strategies (Pennycuik 1978, 1998b, 2008, Nathan et al. 2008, Alerstam 2011, Bauer and Klaassen 2013).

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Supplementary material (Appendix jav-01298 at <www.avianbiology.org/appendix/jav-01298>). Appendix 1–2.