Supplementary material

Appendix 1

Accelerometer data

During the 7 of the 21 trips, acceleration was recorded for each GPS 'fix' over a three second interval at sampling rates of up to 20 times per second. Acceleration components were measured along (x), perpendicular (y) and vertical (z) relative to the tag, i.e. a_x (surge), a_y (sway) and a_z (heave), respectively. To identify flight mode, we determined the average rate of change in heave (ARCH) among the n ~60 measurements within each interval:

$$\text{ARCH} = \overline{|(a_z(\iota + 1) - a_z(\iota))|}, i = 1, n - 1.$$

Flapping flight involved large oscillations (ARCH > 0.35 g, i.e. 0.35 times the acceleration due to gravity), mixed or flap-gliding an intermediate heave (ARCH > 0.1 g) and gliding or floating involved little or no oscillation in heave. Floating was distinguished from gliding by ground speeds < 5 m/s. Typical patterns of each flight mode and of floating are illustrated in Fig. A1. ARCH produces similar classification to that based on overall dynamic body acceleration in the vertical component, odbaZ $= \sum_{i=1}^{n} |a_z - \overline{a_z}|$ (Wilson et al. 2006), but avoids potential misclassifications in cases of slowly varying heave during the interval, e.g. during a turning glide.

Classification of the 462 resulting intervals indicated that while airborne, flapping flight comprised 88.5% flapping, 4.1% gliding and 6.1% flap-gliding (the remaining 1.3% records were not classified). For mixed flight the flapping fraction f_{fl} was estimated from the fraction of overall vertical acceleration between 0.1 g and 0.35 g, i.e. $f_{fl} = 1 - (0.35\text{-ARCH})/0.25$. This resulted in an estimated mean flapping fraction during flap-gliding of 0.49. The overall flapping fraction during flight was then estimated as $f_{fl} = 1 - (0.041 + 0.061 \cdot 0.51)/0.987 = 0.927$. Wind conditions also did not vary significantly when strictly flapping vs. otherwise regarding either tailwind (Kruskal-Wallis test: $\chi^2 = -0.19$, df = 12325, $p = 0.85$) or crosswind ($\chi^2 = 0.89$, df = 13323, $p = 0.37$). There were no significant differences among flight modes regarding unsmoothed airspeed (median airspeeds during

flapping flight $1.14 \cdot V_{mp}$, gliding flight $1.10 \cdot V_{mp}$ and flap-gliding flight $1.20 \cdot V_{mp}$; Kruskal-Wallis test: $\chi^2 = 1.98$, df = 409, p = 0.37).

Appendix 2

Uncertainty analysis maximum-range airspeeds

Measured airspeeds or ground speeds are often analysed relative to tailwind and crosswind components (e.g. Safi et al. 2013, Sapir et al. 2014b). However, while the effect of uncertainty in preferred direction on perceived instantaneous flow assistance has been tested (Kemp et al. 2012), the effect on (predicted)airspeed of defining tailwinds relative to presumed goal directions (e.g. Liechti 1995, Sapir et al. 2014a), estimated flight headings (Karlsson et al. 2010b, McLaughlin and Montgomerie 1990) or track directions (Safi et al. 2013) has not been addressed.

Figure A2 depicts contours of predicted (maximum-range) airspeed under various assumptions about transport cost minimization as a function of tailwind and crosswind strength. All wind and flight speeds are scaled to the minimum power speed V_{mp}. Maximum-range airspeeds based on FC are similar when assuming minimization of transport costs along preferred i.e. goal directions (Fig. A2a) and along directions of heading (Fig. A2b). However, GO individuals minimizing costs along the track direction (Fig. A2c) yield maximum-range speeds which decrease rather than increase in very strong headwinds relative to the goal and remain constant or decrease as opposed to increase in crosswinds. In other words, if birds are actually fully drifting (as per GO) and we analyse airspeed in relation to track directions, the relation of airspeed to (apparent) tailwind and crosswind will be contrary to what is normally expected.

Appendix 3

Sensitivity analysis

To test whether sinuosity of trajectories affected overall flight efficiency we determined median sinuosity for each trip, as defined by the ratio of the path length of three consecutive segments to the straight-line distance (Dutton 1999, Laube and Purvis 2011). Trajectories pooled among all 21 trips

were characterized by highly directed movement i.e. low sinuosity (median SV = 0.23, see Dutton 1999), but 1 trip exhibited moderate sinuosity (0.33 > SV ≥ 0.67), and 5 trips high sinuosity (SV > 0.67). Sinuosity did not differ between trips with low and high resolution data (mean sampling rates less than or exceeding 7.5 minutes, respectively; Mann–Whitney–Wilcoxon test: Z = 0.04, p = 0.97).

To test the effect of not having measurements of wing surface area and wing span for each tagged individual, we calculated predicted maximum-range speeds for windless conditions, V_{mr0}, over the range of wingspans in Cramp and Simmons (1983), scaling wing surface area according to wingspan squared (Pennycuick 2008). Resultant values differed from those assuming a standard wingspan and wing surface area as used in the simulations (1.43 m and 0.243 m^2, respectively; Bruderer and Bolt 2001) by at most 4%.

We also simulated all 21 trips for each orientation strategy based on doubled body drag coefficients ($C_{db} = 0.2$), which presumably severely overestimates the influence of the UvA-BiTS loggers (cf. Obrecht et al. 1988, Wilson et al. 2004). This resulted in lower predicted maximum-range airspeeds but also lower minimum-power airspeeds, whereby median predicted airspeeds were similarly scaled to V_{mp}: for OO 1.45 vs. 1.42 with standard drag coefficient, for FC 1.48 vs. 1.52, and for GO 1.49 vs. 1.52. Measured airspeeds relative to predicted V_{mp} were higher with doubled body drag (1.34 vs 1.12) but remained over-predicted by the simulations (Kruskal-Wallis test: mean ranks V_a, 1718, V_{OO}, 2487, V_{FC}, 4812 and V_{GO}, 5187, $p < 10^{-16}$).

Note that although we did not simulate mass loss during active flight (which was maximally 9.4 hours), birds typically lose about 1% mass per hour to mechanical energy expenditure (Delingat et al. 2008, Hussell and Lambert 1980). This would change predicted maximum-range speeds (in windless conditions) by maximally 4% compared to estimates based on weight at capture. Therefore, this is presumably a much smaller factor than the uncertainty due to fluctuations of body mass over the migrating and breeding season.

Finally, we estimated deviations from actual headings based on ground speeds calculated using next location data as opposed to the Doppler-based instantaneous GPS measurements (Safi et al. 2013). This did not strongly influence estimated headings or airspeeds: median deviation from OO was 26˚ (vs. 25˚ using instantaneous measurements), from FC 30˚ (vs. 34˚) and from GO 37˚ (vs. 43˚), and median airspeed relative to V_{mp} was 1.04 (vs 1.12).
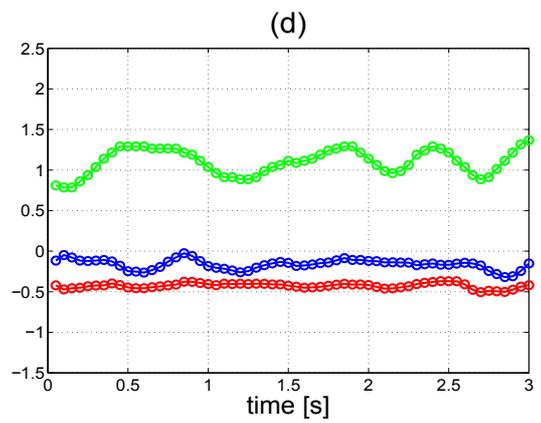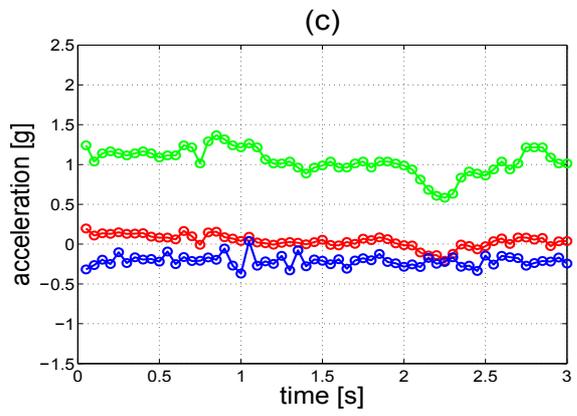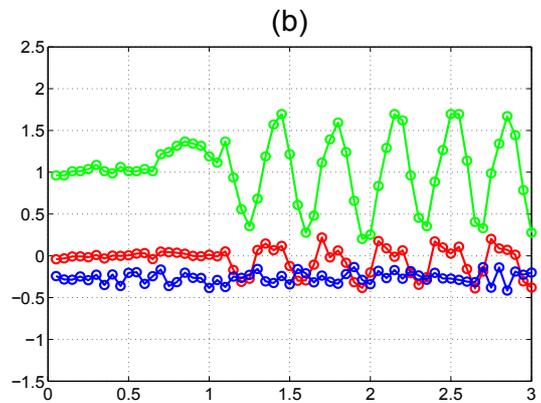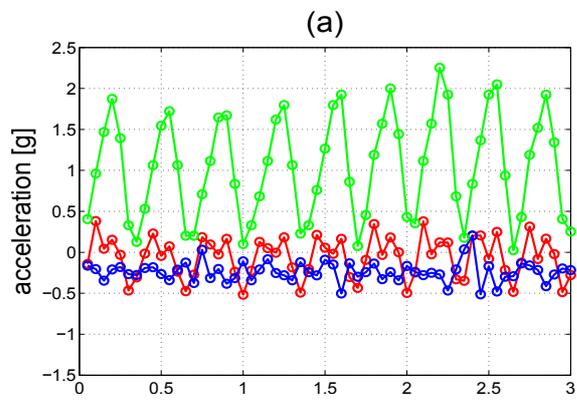
Figure A1: Three-second time series of acceleration (in units of acceleration due to gravity, $g = 9.8\ ms^{-2}$), illustrating the four basic modes of movement during travel (a) flapping flight, characterised by large oscillations in the vertical component relative to the tag (heave, green lines) compared to the horizontal components (surge in red, sway in blue), (b) gliding, characterised by virtually no oscillation, (c) mixed or flap-gliding flight, characterised by a transition from flapping to gliding flight and (d) floating, characterised by gentle oscillations in all three components (but also lower ground speeds than gliding, not illustrated)
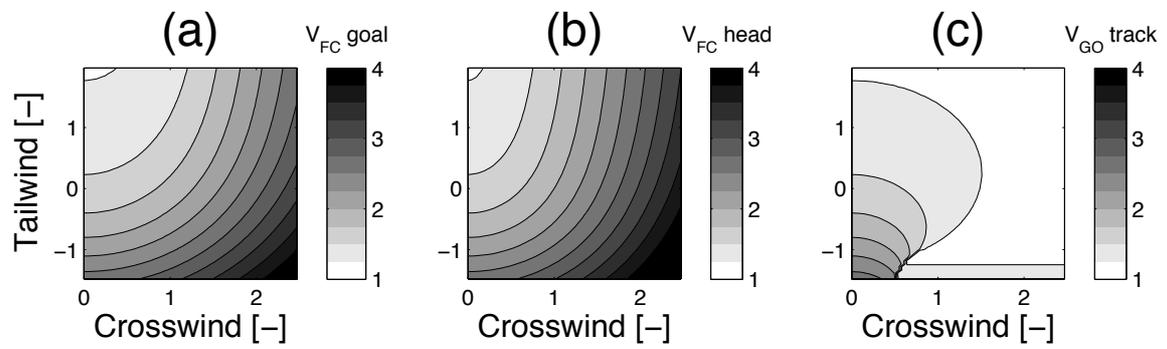
Figure A2: Predicted maximum-range airspeed as a function of tailwind and crosswind strength based on (a) FC and minimization of transport costs along preferred (goal) directions, (b) FC and minimization of transport costs along directions of heading and (c) GO and minimization of transport costs along track directions. Both airspeeds and wind speeds are scaled to the minimum-power speed V_{mp}

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