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DOI

[10.1111/jav.00828](https://doi.org/10.1111/jav.00828)

Publication date

2016

Document Version

Final published version

Published in

Journal of Avian Biology

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Citation for published version (APA):

McLaren, J. D., Shamoun, J., Camphuysen, C. J., & Bouten, W. (2016). Directed flight and optimal airspeeds: homeward-bound gulls react flexibly to wind yet fly slower than predicted. *Journal of Avian Biology*, 47(4), 476-490. <https://doi.org/10.1111/jav.00828>

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Directed flight and optimal airspeeds: homeward-bound gulls react flexibly to wind yet fly slower than predicted

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Birds in flight are proposed to adjust their body orientation (heading) and airspeed to wind conditions adaptively according to time and energy constraints. Airspeeds in goal-directed flight are predicted to approach or exceed maximum-range airspeeds, which minimize transport costs (energy expenditure per unit distance) and should increase in headwinds and crosswinds. Diagnosis of airspeed adjustment is however obscured by uncertainty regarding birds' goal-directions, transport costs, interrelations with orientation strategy and the attainability of predicted behaviour. To address these issues, we tested whether gulls minimized transport costs through adjustment of airspeed and heading to wind conditions during extended inbound flight over water (180–360 km) to their breeding colony, and introduce a methodology to assess transport (energy) efficiency given wind conditions. Airspeeds, heading, flight mode and energy expenditure were estimated using GPS tracking, accelerometer and wind data. Predicted flight was determined by simulating each trip according to maximum-range airspeeds and various orientation strategies. Gulls employed primarily flapping flight (93%), and negotiated crosswinds flexibly to exploit both high altitude tailwinds and coastal soaring opportunities. We demonstrate that predicted airspeeds in heavy crosswinds depend strongly on orientation strategy and presumed preferred direction. Measured airspeeds increased with headwind and crosswind similarly to maximum-range airspeeds based on full compensation for wind drift, yet remained ~ 30% lower than predicted by all strategies, resulting in slower and 30–35% costlier flight. Interestingly, more energy could be saved through adjustment of airspeed (median 40%) than via orientation strategy (median 4%). Therefore, despite remarkably flexible reaction to wind at sea, these gulls evidently minimized neither time nor energy expenditure. However, airspeeds were possibly over-predicted by current aerodynamic models. This study emphasizes the importance of accounting for orientation strategy when assessing airspeed adjustments to wind and indicates that either the cost or adaptive 'currency' of extended flight among gulls may require revision.

Reaction to wind

Adaptation of efficient flight is essential to volant creatures (Norberg 1990, Hedenström and Alerstam 1995, Lentink et al. 2010, Baird et al. 2011, Sterbing-D'Angelo et al. 2011). When birds undertake goal-directed flight between two locations, for example during central-place foraging or migration, their reaction to wind will impact their time and energy expenditure (Houston 2006, Alerstam 2011). Strategies to negotiate wind should therefore depend on a bird's navigational and flight capabilities, its ability to gauge and predict prevalent flow conditions and constraints on time and energy expenditure (Nathan et al. 2008, Alerstam et al. 2011). Adaptation regarding a given mode of activity (e.g. migratory flight) will naturally be driven by its relative contribution to fitness within the annual routine (McNamara and Houston 2008) and ultimately constrained by both individual experience (Alert et al. 2015, Mitchell et al. 2015) and phylogenetic processes (Gould and Lewontin 1979, McNamara et al. 2001).

How might we therefore expect birds to fly in variable and at least partly unpredictable wind conditions? Birds in flight can react to wind by adjusting the orientation of their horizontal body axis (hereafter, heading) or their self-propelled speed (hereafter, airspeed) to experienced and anticipated conditions (Liechti 1995, Kemp et al. 2012, McLaren et al. 2014, Nilsson et al. 2014 and see Table 1 for terms relevant to this study). A simplifying approach is to assume that birds adjust their flight to optimize some 'currency' of movement as a proxy for fitness, for example time or energy expenditure, predation risk or rate of energy gain (McNamara and Houston 1986, Hedenström and Alerstam 1997).

Orientation strategies

A well-studied case is to assume that birds adjust their flight orientation to wind in order to minimize time expenditure to a specific goal (Alerstam 1979a, 2011, Houston 2006). To the extent that airspeeds remain constant, time-minimizing orientation also minimizes total energy expenditure. Many

Table 1. Names and descriptions of terms relevant to orientation and reaction to wind in goal-directed flight.

Term	Description
Airspeed	self-propelled speed relative to the moving air
Crosswind	component of horizontal wind speed perpendicular to a given goal direction
Full compensation	adjustment of heading (and possibly airspeed) to counteract crosswind drift, resulting in a constant direction of travel
Full drift	non-adjustment of heading to a fixed (goal) direction
Goal orientation	continual (re-) adjustment of heading to current goal direction
Heading	angle between the horizontal body axis and goal direction
Maximum-range airspeed	airspeed resulting in lowest transport cost, i.e. mechanical energy expenditure per unit distance (J m^{-1})
Minimum-power airspeed	airspeed resulting in lowest rate of mechanical energy expenditure (J s^{-1})
Optimal orientation	adjustment of heading to minimize trip-total time expenditure
Overcompensation	adjustment of heading resulting in travel against the crosswind direction
Overdrift	heading partially with the wind, increasing drift relative to full drift
Partial compensation	adjustment of heading resulting in some fraction of drift compared to full drift
Tailwind	component of horizontal wind speed parallel to a given goal direction

orientation strategies are predicted to be close to time-optimal when winds are overall weak compared to airspeeds, (McLaren et al. 2014). In strong but spatiotemporally uniform winds, full compensation for wind drift (FC) – where feasible – minimizes both time and energy expenditure. This involves adjusting the heading windward to maintain a direct course to the goal. Contrastingly, goal orientation (GO) involves continually heading towards the goal i.e. fully drifting with the wind. Goal orientation is inefficient in strong uniform flow since it results in encountering increasingly strong headwinds (or weaker tailwinds) on approach to the goal (Alerstam 1979a, where GO is termed full drift). Partial compensation involves adjustment of heading resulting in – for a given airspeed – some fraction of drift relative to full drift (Kemp et al. 2012).

More generally, the time-minimizing solution for orientation in any time-varying horizontal flow (hereafter, optimal orientation, OO) was recently calculated for animal movements based on fixed swimming speeds or airspeeds (Hays et al. 2014, McLaren et al. 2014). This solution, which would involve complete knowledge of current and future flow conditions en route, has been proposed as a benchmark for assessing flight performance (McLaren et al. 2014). Resulting solutions for optimal orientation can involve both overdrift (heading partially downwind) and over-compensation. Measured flight orientation sometimes suggests flexible patterns involving overcompensation and overdrift across entire routes (e.g. among migrating raptors, Klaassen et al. 2011 and among foraging bats, Sapir et al. 2014b), but generally emphasize partial and full compensation (Green et al. 2004, Karlsson et al. 2010a, Sapir et al. 2014a, Chapman et al. 2015). Birds can, under certain tailwind conditions, also exploit vertical wind structure by combining drift at high altitudes with over-compensation at low altitudes (Alerstam 1979b), or by taking advantage of high-altitude tailwinds in trade-wind zones (Schmaljohann et al. 2009) or frontal systems (Gauthreaux 1991, Dokter et al. 2013).

Optimal airspeeds

Choice of airspeed should depend on the relative importance of energy expenditure and deposition specific to a given activity (Hedenström and Alerstam 1995, Houston 2006). Mechanical energy expenditure during flight typically fol-

lows a convex, typically U-shaped, curve with respect to airspeed (hereafter, ‘power curve’), which varies according to body morphology and air density (Askew and Ellerby 2007, Pennycuick 2008). During commuting and migratory flights, airspeeds are expected to equal or exceed the maximum-range speed, which minimizes transport costs, i.e. energy expenditure per unit distance (Hedenström and Alerstam 1995). When the cost of replenishment of resources is critical in addition to transport costs, airspeeds higher than maximum-range speeds are predicted, as for example during chick-provisioning (Houston 2006) or migration involving stopover bouts (Hedenström and Alerstam 1998). Airspeeds lower than maximum-range speeds have only been predicted for foraging or song flight as opposed to goal-directed flight (Hedenström and Alerstam 1994, 1995) or for some cases of fly-foraging migration, which combines goal-directed flight and sporadic foraging without extended stopover (Strandberg and Alerstam 2007, Alerstam 2011). In the most extreme case where the urge to forage completely outweighs that to relocate, a bird should minimize instantaneous power expenditure by flying at its minimum-power airspeed, which is lower than the maximum-range airspeed (Hedenström and Alerstam 1995).

While minimum-power speeds are invariant to wind conditions, maximum-range speeds vary with incident wind, specifically to decrease in increasing tailwinds and to increase in increasing crosswinds (Liechti 1995). However, these adjustments should also depend on the orientation strategy adopted. For example under full compensation for wind drift, maximum-range airspeeds will exceed those under full drift or under adaptive drift strategies (cf. Pennycuick 1975, Liechti et al. 1994, Liechti 1995). The extent to which a bird adjusts its airspeed to incident wind conditions should therefore depend on both its priority to reach a destination and its corresponding orientation strategy regarding wind.

Studies which addressed the effect of wind on goal-directed flight generally found clear relationships between airspeed and tailwind components but either found less clear relationships with respect to crosswinds (Hedenström et al. 2002, Safi et al. 2013, Sapir et al. 2014a, Elliott et al. 2014a, Mitchell et al. 2015), did not explicitly account for crosswind effects (Able 1977, Schnell and Hellack 1979, Welham 1994, Spear and Ainley 1997, Yoda et al. 2012) or ignored crosswinds altogether (McLaughlin and Montgomerie 1990,

Pennycuick et al. 2013). Most studies further indicated that airspeeds ranged between minimum-power and maximum-range airspeeds, suggesting a compromise between minimizing instantaneous (metabolic) and transport costs. This further suggests that either these flights were not entirely goal-directed (e.g. fly-foraging) or that the adaptive benefit of minimizing transport costs is insufficient compared to other adaptations. For example, chick-provisioning murrelets *Uria lomvia* and kittiwakes *Rissa tridactyla* were shown to adjust not only their airspeed but also their choice of prey to maintain chick-provisioning rates in variable wind conditions (Elliott et al. 2014a).

However, several uncertainties remain which may have partially contributed to apparent mismatches between proposed and measured behaviour. Firstly, many studies accounting explicitly for crosswinds defined wind components relative to track directions (Hedenström et al. 2002, Safi et al. 2013, Elliott et al. 2014a, Sapir et al. 2014a) or fixed geographic axes (Nilsson et al. 2014, Mitchell et al. 2015) rather than relative to actual headings or individual goal directions. As a result, if wind drift occurred, crosswind effects could have been misclassified as tailwind effects and vice-versa. Interestingly, an early study found tailwind relative to heading to be the best predictor of airspeed (Able 1977), and a more recent study on migrating common swifts *Apus apus* found a significant relation between airspeed and crosswind relative to headings (Karlsson et al. 2010b). Second, birds flying above clouds or over water have been proposed to have difficulty in orienting or gauging incident wind (Alerstam and Pettersson 1976, Bingman et al. 1982, Sjöberg et al. 2015). Lastly, the cost of flight has been chiefly modelled using aerodynamic models which are far from certain regarding parameterization (Askew and Ellerby 2007, Pennycuick et al. 2013) and even the functional form of the power curve itself (Rayner 1994, 2001, Muijres et al. 2012). For example, parametrization of power curves for larger birds such as gulls is based largely on field experiments, where both wind effects and the relation between actual and optimal speeds are uncertain (Pennycuick 1997).

Current study

In this paper we test whether gulls undertaking extended flight to a specific goal minimize transport costs through adjustment of airspeed and heading to wind conditions. We analysed reaction to wind by GPS-tagged lesser black backed gulls *Larus fuscus* during extended flights (180–360 km) on return to their breeding colony (Camphuysen 2013). Gulls employ a variety of flight modes, including flapping, soaring and mixed or flap-gliding flight (Baudinette 1974, Woodcock 1975), but few scientific studies have addressed their relative use. Lesser black-backed gulls are known to perform flapping flight during cruising flight (Pennycuick 1987) and during migration over ecological barriers (Schmaljohann et al. 2008) but also use soaring and gliding flight (including flap-gliding and slope-soaring) when above land outside migration (Shamoun-Baranes and van Loon 2006).

To further reduce the possibility of interim goals and of soaring, i.e. of indirect orientation, we restricted analysis to extended flights over water between England and the breeding colony in the Netherlands. This furthermore ensured

our being able to correctly diagnose reaction to tailwind and crosswind components in relation to a known destination. When winds blow onshore towards the Netherlands, it is possible that gulls may alter their orientation to take advantage of slope-soaring along the coast (hereafter, coastal soaring). The accelerometer data furthermore provided an opportunity to quantify incidence of flight mode by gulls during their goal-directed flights over water (Bouten et al. 2013).

Airspeeds and headings were estimated from the tracking data using wind data from a mesoscale model and compared with predicted airspeeds and headings, which were simulated using individual-based modelling techniques according to optimal orientation (OO), full compensation for drift (FC) and goal orientation (GO). For each orientation strategy, we derived appropriate wind-adjusted maximum-range airspeeds given tailwind and crosswind conditions along simulated flight paths. We further tested whether adjustments relative to track as opposed to goal directions can lead to spurious interpretation (pseudo-compensation) when birds drift in strong crosswinds. By comparing actual to predicted optimal energy expenditure during flight in given wind conditions, this study provides a first assessment of travel efficiency of directed flight in terms of energy expenditure (hereafter energy efficiency). Energy expenditure was recently proposed to be the primary ‘currency’ of migration among lesser-black-backed gulls (Klaassen et al. 2012). Finally, the relative extent to which adjustment of heading and airspeed reduce energy expenditure has not been addressed. We therefore simulated each orientation strategy at fixed airspeeds, based on maximum-range airspeeds as calculated in the absence of wind.

We specifically hypothesize that during directed flight, the gulls will exhibit: 1) enhanced wind drift a) at higher altitudes in tailwinds (Alerstam 1979b) and b) in onshore winds relative to the Dutch coast; 2) headings otherwise resembling either time-optimal orientation (OO) based on fixed airspeeds, or other near-optimal strategies (McLaren et al. 2014); 3) airspeeds approaching or exceeding predicted maximum-range airspeeds which increase with both headwind and crosswind (Hedenström and Alerstam 1995, Liechti 1995); and 4) prioritization of minimizing energy as opposed to time expenditure, i.e. closer to optimal energy efficiency than time efficiency given wind conditions (Klaassen et al. 2012, McLaren et al. 2014).

We then discuss results in the context of adaptation to wind, currency of travel and implications for analysing reaction to wind.

Methods

Measurements and flight analysis

Between 2008–2013, 51 lesser black-backed gulls from a breeding colony on the island of Texel in the Netherlands (53°N, 4.7°E) were fitted with 18 g UvA-BiTS GPS loggers (Bouten et al. 2013, Camphuysen 2013). This provided measurements of position, altitude, ground speed and – during some flights – tri-axial acceleration. These data can together be used to distinguish between modes of movement, e.g.

floating, flapping and gliding (see Fig. 2 in Bouten et al. 2013). Sampling intervals were varied remotely to either 5 or 20 min depending on solar radiation and battery status. We examined extended flights from 2013, during which six tagged individuals returned to the colony via England during spring migration, after which five individuals completed one or more commuting flights to England and back. These extremely long commuting flights make up less than 1% of all central-place foraging flights from this colony and involved only non-breeding individuals in 2013 (see chapter 8 in Camphuysen 2013). From a total of 25 flights occurring in 2013, 21 were kept for analysis (summarized in Table 2) of which 5 were migratory flights (labelled with an M). The four additional inbound trips from England were excluded following preliminary analysis: two trips due to extensive (foraging) diversions at sea, one trip due to ship-following

(diagnosed by repeated slow and straight trajectories in odd directions) and one trip due to having only one measurement over water.

Horizontal ground speed vectors were obtained directly via instantaneous Doppler shift measurements on the GPS rather than via next location measurements (Bouten et al. 2013, Safi et al. 2013). Floating records were identified either by accelerometer measurements (see below) or by ground speeds below 2.5 m s^{-1} and altitude measurements below 2 m (Shamoun-Baranes et al. 2011). These were subsequently removed from analysis, i.e. only measurements and times attributable to actual flight were used to estimate orientation, airspeeds and time and energy expenditure. For each trip, starting points for analysis and simulations were chosen at points prior to departure from the coast of England, except in two cases (trips 1 and 16, Table 2). For

Table 2. Relevant details from all 21 trips made by lesser black-backed gulls in 2013 between England and their breeding colony on Texel in the Netherlands. Flight durations are excluding floating time, mean duration between GPS fixes Δt is in minutes, altitudes are smoothed, negative values of crosswind components W_C are to the right, i.e. southward, and airspeeds V_a are equivalent airspeeds, i.e. scaled to sea level. Arrival and departure times within 2 h of civil dusk and dawn are marked in boldface, and nocturnal departures and arrivals by underlined boldface.

Trip number ¹	Logger and ring ID, sex, weight [kg]	Distance [km]	Departure date and time	Arrival date and time	Trip (flight) duration [h]	No. GPS fixes, Δt [min]	Med. and max altitude [m]	Median W_C , W_C [m s ⁻¹]	Median and max V_a [m s ⁻¹]
1 M	534, FAPP ♀ 0.68	184	18 March 09:09:20	18 March 15:47:44	6.6 (4.6)	16, 24	40, 510	5.5, 2.6	11.6, 15.5
2	534	198	12 April 15:25:13	12 April 19:18:50	3.9 (3.6)	9, 24	390, 470	7.3, 1.3	11.6, 12.6
3 M	537, MACV ♂ 1.01	349	2 March 11:00:34	3 March 18:44:33	7.7 (7.4)	22, 20	100, 380	4.2, -1.6	9.8, 11.0
4	537	218	29 March 16:45:38	30 March 05:06:52	12.4 (8.6)	33, 23	0, 160	-5.4, -2.4	12.6, 16.0
5	537	222	23 April 11:23:56	23 April 14:30:20	7.3 (3.4)	36, 6	690, 870	8.8, -2.0	12.3, 14.0
6	537	223	3 May 19:37:26	4 May 00:10:09	4.6 (4.3)	53, 5	30, 480	2.9, 5.9	11.8, 15.2
7 A	537	218	21 May 18:48:55	22 May 05:02:30	10.2 (7.8)	111, 5	0, 30	-1.4, -10.0	13.6, 19.5
8 A	537	206	25 May 15:02:30	25 May 21:48:01	6.8 (6.6)	67, 6	130, 600	-4.3, -10.6	14.5, 17.2
9 A	537	218	10 June 20:23:09	11 June 07:27:26	11.1 (6.1)	111, 6	20, 190	-1.0, 1.5	11.5, 13.9
10 A	537	358	29 June 15:16:38	29 June 22:14:44	7.0 (6.8)	79, 5	210, 770	3.4, 1.8	11.1, 13.8
11 M	540, MAPM ♂ 0.895	204	8 May 23:42:44	9 May 03:05:38	3.4 (3.4)	11, 20	50, 90	10.6, 3.0	8.1, 14.1
12 M	608, FARB ♀ 0.74	218	2 March 17:10:10	3 March 11:27:19	18.3 (9.4)	45, 22	20, 230	0.3, -3.9	10.3, 15.6
13		223	14 April 14:02:09	15 April 05:58:29	15.9 (4.8)	46, 21	300, 1240	6.2, 16.5	11.7, 21.5
14	757, FARA ♀ 0.735	209	23 April 19:04:09	24 April 00:26:01	5.4 (3.7)	65, 5	90, 360	4.4, 1.2	12.5, 17.0
15	757	214	28 April 07:55:14	28 April 12:55:49	4.9 (4.4)	61 (5)	110, 210	5.4, 3.0	10.3, 12.0
16	757	235	8 May 17:35:09	9 May 03:09:21	9.6 (6.2)	114 (5)	440, 1240	10.4, 3.6	9.6, 12.5
17	757	195	11 June 05:21:31	11 June 17:15:22	11.9 (6.5)	138 (5)	30, 130	0.7, 4.1	10.3, 13.3
18 A	757	212	18 June 18:09:26	19 June 06:21:44	12.2 (4.8)	184 (5)	20, 160	1.2, -0.3	9.8, 15.4
19 A	757	202	29 June 15:51:56	29 June 20:43:27	4.9 (4.8)	58 (5)	280, 1040	1.7, -4.9	10.3, 12.2
20 M	782, FARK ♀ 0.745	267	7 April 03:58:40	7 April 11:01:06	7.1 (6.0)	22 (20)	230, 400	1.7, 0.7	9.6, 12.7
21 A	782	249	29 June 17:31:13	29 June 23:14:48	5.7 (5.2)	68 (5)	230, 400	4.0, 1.5	11.0, 13.3

¹A and M denote flights with accelerometer data during migration respectively.

these two trips, we chose to start analysis at points (3 and 40 km) off the coast of England where flight was resumed following extended floating.

Estimated airspeed and heading (hereafter, measured airspeed and heading) were determined by subtracting the estimated horizontal wind vector from the measured ground speed vector. Incident wind was estimated using ECMWF Deterministic model u and v wind components and geopotential height data at the surface and 4 standard pressure levels (1000 mb, 925 mb, 850 mb and 700 mb) and at 0.25° and 3 h resolution (Dee et al. 2011). The ECMWF data were linearly interpolated to the altitude, position and time of each record. In order to directly compare results from all individuals, we scaled airspeeds and incident wind conditions for each individual to its minimum power airspeed, V_{mp} . This accounted for both the effect of body size on airspeed (males being heavier and therefore faster than females, Alerstam et al. 2007, Camphuysen 2013 and Table 2) and also the relative strength of experienced winds for each individual. Airspeeds were also converted to equivalent airspeeds at sea-level pressure to account for air density effects (see section 3.4 in Pennycuik 2008 and Eq. 10 in Schmaljohann and Liechti 2009). To alleviate potential inaccuracies of the GPS measurements, altitudes and resultant airspeeds were smoothed using a 5-span moving average. Differences regarding median tailwind and crosswind strength (absolute crosswind speed) between migratory and commuting trips were assessed using the Mann–Whitney–Wilcoxon test.

Incidence of flight mode during the 7 trips with acceleration data (labelled with A in Table 2) was assessed via changes in the vertical (heave) acceleration component as derived from the tri-axial accelerometer (Wilson et al. 2006, Shamoun-Baranes et al. 2012). In Supplementary material Appendix 1 we describe how we classified flight mode and estimated the flapping ratio for each GPS measurement, the overall mean of which was used to estimate overall energy expenditure per trip. Differences among flight modes regarding airspeed and wind conditions were assessed using the Kruskal–Wallis nonparametric test.

Predicted airspeed vs wind

In the absence of or ignoring wind conditions, the maximum-range airspeed, V_{mro} , minimizes transport cost $T(V_a) = P(V_a)/V_a$ where $P(V_a)$ is the required mechanical power ($J s^{-1}$) to fly at a given airspeed V_a (Pennycuik 2008). Maximum-range airspeeds will depend on incident wind conditions (Pennycuik 1975, Liechti et al. 1994) but also on the orientation strategy (heading) and the direction along which transport cost is minimized. For example, always heading downwind will produce the absolute minimum transport costs along the resultant ‘track’ direction but disregards any crosswind drift relative to a given goal. A seemingly appropriate choice for directed flight is to consider minimization of transport costs along a preferred direction:

$$T_G(V_a) = \frac{P(V_a)}{V_g \cos \partial} = \frac{P(V_a)}{W_T + V_a \cos \psi} \quad (1)$$

where V_g is the resultant ground speed, W_T the tailwind component and ∂ and ψ the angles of drift and heading

relative to the preferred direction, respectively. This measure of transport cost was suggested by McLaren et al. (2014) and is equivalent to previous definitions in the limiting cases of full drift or goal orientation $\psi = 0$, i.e. heading in the preferred direction (Pennycuik 2008) and full compensation for drift $\psi = -\sin^{-1}(W_c/V_a)$, where W_c is the crosswind component relative to the goal direction (Liechti et al. 1994).

To elucidate the predicted effect of orientation strategy on airspeed, we determined maximum-range airspeeds in synthetic wind conditions for goal-orienting individuals (V_{GO}) and for fully compensating individuals (V_{FC}) assuming they minimized transport costs along preferred (goal) directions (Eq. 1). In Supplementary material Appendix 2 we further explore whether assuming that birds react to wind relative to track directions (as opposed to headings or goal direction) impacts the perceived relationship between airspeeds and tailwinds and crosswinds. In all cases, tailwind and crosswind were varied in increments $\Delta W = 0.1 m s^{-1}$ up to absolute values of $20 m s^{-1}$, i.e. about double the minimum power speed. For this calculation, we estimated mechanical energy expenditure of a gull flying at a pressure level of 1000 mb following Pennycuik (2008), with an updated induced power factor of $k = 0.9$ to account for flexible wing morphology (Pennycuik et al. 2013). We chose a mass of 0.745 kg (capture weight of individual FARK, representing the median mass among the five individuals, Table 2) and a wing length and wing surface area of 1.43 m and 0.243 m², respectively (Bruderer and Boldt 2001).

Flight simulations

For each trip, we simulated flight using ECMWF wind data and wind-adjusted maximum-range speeds and three generic orientation strategies, which represent extremes in orientation assuming fixed airspeeds: 1) optimal orientation (OO), which minimizes flight duration for a given (fixed) airspeed and presumes perfect knowledge of present and future wind and position (McLaren et al. 2014), 2) full compensation for wind drift (FC), which presumes perfection in gauging and compensating for lateral wind displacement and 3) goal orientation (GO), which involves full drift towards a continually updated preferred direction and presumes perfection in gauging goal directions but no need to gauge incident wind. For each orientation strategy, flight based on wind-adjusted airspeeds was simulated using the individual-based model described in McLaren et al. (2014) with 2 min time steps. Maximum-range airspeeds were determined using Eq. 1 given respective wind and headings. With OO, optimal headings for subsequent time steps were updated using Eq. 2.6 in McLaren et al. (2014). To assess the effect of adjusting airspeed to wind conditions on flight performance, we also simulated each trip and orientation strategy based on maximum-range airspeeds ignoring wind, V_{mro} . Initial OO headings were solved using search methods as described in McLaren et al. (2014).

For simplicity we simulated flight at a single pressure level for each trip, according to median and maximal flight altitudes per trip (Table 2). For most (16 of 21) trips we chose simulations using wind data at the 1000 mb pressure level (ca 100 m a.s.l.). We further used 2 m wind data for one trip (trip 11, where flight remained below 30 m), and wind

data at 925 mb (ca 850 m a.s.l.) for four trips (trips 5, 13, 16 and 19) for which smoothed flight altitudes approached or exceeded 800 m.

In order to directly compare simulated and actual trips (which naturally will not coincide), we simulated flight to the goal starting from each measured location of each trajectory beyond 7.5 km distance from the colony (totalling 880 simulations per orientation strategy). In this way, predicted headings and airspeeds for each strategy were obtained for each measured time and horizontal location. Lastly, to facilitate computations, simulations were terminated when simulated individuals arrived on land within 5 km of the colony.

Comparison of measured and predicted flight

Flight orientation was assessed, at each GPS measurement, in two ways: by fractional compensation for wind drift, f_c , estimated by the proportion of actual drift relative to full drift (Green and Alerstam 2002, Kemp et al. 2012), and by the deviation (absolute difference) in heading between each predicted orientation strategy and the estimated actual heading. To avoid misleading values in the near-absence of crosswinds, fractional compensation was only analysed when full drift would result in a drift angle exceeding 10° .

To test hypothesis 1a, that gulls would in tailwind conditions drift at high and (over-) compensate at low altitudes (sensu Alerstam 1979b), we assessed the extent to which fractional compensation, f_c , and wind conditions varied between trips with median flight altitudes above and below 200 m, respectively (hereafter, 'high' and 'low' flights; maximal altitudes of flapping flight among radar-tracked lesser black-backed gulls averaged 175 m in Shamoun-Baranes and van Loon 2006). To account for the fact that wind strength generally increases with altitude, for both 'low' and 'high' flights we compared experienced winds below 200 m (each trip naturally began and ended close to the earth's surface).

We also tested whether birds preferentially drifted towards the Dutch coast when winds were favourable for coastal soaring (hypothesis 1b). Given that the breeding colony is situated at the northernmost point of a nearly north-south aligned coast and that initial goal directions generally approximated due east, we compared fractional compensation in onshore winds towards the south ($u > 0$ and $v < 0$, hereafter, onshore winds) and other scenarios (hereafter, offshore winds).

Deviations from predicted headings (hypothesis 2) for FC were based on measured as opposed to maximum-range airspeeds and for OO were based on maximum-range airspeeds, V_{OO} . Predicted headings with GO, being based on goal directions, were independent of airspeed.

We compared measured and predicted airspeeds (hypothesis 3) as a function of incident tailwind and crosswind to maximum-range airspeeds based on windless conditions (V_{mro}) and on reaction to incident wind according to each simulated orientation strategy (V_{OO} , V_{FC} and V_{GO}). We also tested whether measured airspeeds in weak winds more closely resembled predicted maximum-range speeds based on windless conditions (V_{mro}) as opposed to minimum-power airspeeds (V_{mp}). We made this comparison whenever experienced wind speeds were less than 25% of V_{mp}

(wind-adjusted maximum-range airspeeds in these winds differed from V_{mro} by maximally 7%).

To test whether gulls prioritized energy over time expenditure (hypothesis 4), we estimated their efficiency of time and energy expenditure. An optimal time and energy benchmark for each trip was computed as the lowest time and energy expenditure among all simulations. Efficiency of actual flight was calculated for each trip as the ratio of the benchmark to the (estimated) actual expenditure. Similarly, the efficiency of each strategy regarding time and energy expenditure was calculated relative to the appropriate benchmark. We estimated an upper bound for the actual mechanical energy expenditure by assuming flapping flight throughout a trip (with expenditure at airspeeds below V_{mp} set to $P(V_{mp})$). A lower bound for energy expenditure was estimated by assuming 1) that mechanical energy costs for gliding flight and acceleration within flap-gliding cycles were negligible (cf. Rayner et al. 2001, Muijres et al. 2012), i.e. that energy expenditure was proportional to the estimated overall flapping fraction, f_{fl} , and 2) for flight along the coast of the Netherlands, that slope-soaring was always possible at a mechanical energy cost of twice the basal metabolic rate (Lasiewski and Dawson 1967, Hedenström 1993). We assumed that basal metabolic costs were the same on arrival as during flight and therefore not relevant to energy efficiency (i.e. these rates were only used to estimate the equivalent mechanical cost during slope-soaring). Note that predicted airspeeds would increase when accounting for metabolic costs.

In Supplementary material Appendix 3 we outline the sensitivity analysis which considers: 1) straightness of trajectories to confirm directedness of flight, whereby assessing efficiency of goal-directed flight is meaningful, 2) uncertainty in wing measurements, 3) the effect of using instantaneous GPS as opposed to next-location ground speed measurements, and 4) the effect of both increased drag from the logger and of ignoring loss of mass en route on predicted airspeeds.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.7vs7r>> (McLaren et al. 2015).

Results

Measurements and flight analysis

The gulls exhibited flexibility in departure and arrival times, flight altitudes and duration of floating bouts (Table 2). Initial great circle distances from the colony varied from 184 to 358 km (median 218 km). Departures from England and arrivals at the colony occurred at all times of day, but typically during daylight hours. The median (smoothed) flight altitude was 101 m with trip-maximal altitudes of 90–1240 m (median 395 m). Many trips involved extended floating (0–11.4 h per trip, median 1.0 h). Excluding floating, flight durations ranged from 3.4–9.4 h (median 5.2 h), with trip-mean ground speeds ranging from 23–66 km h⁻¹ (grand mean 47 km h⁻¹). Trip-median equivalent airspeeds (i.e. at sea-level pressure) ranged from 8.1 to 14.5 m s⁻¹ (Table 2) or relative to each individual's estimated minimum-power speed, 0.8 to 1.4 · V_{mp} . Pooled from all flights, overall median

equivalent airspeed was 11.3 m s^{-1} ($1.12 \cdot V_{mp}$) with 5th and 95th percent quantiles of 7.9 m s^{-1} and 15.1 m s^{-1} ($0.74 \cdot V_{mp}$ and $1.49 \cdot V_{mp}$), respectively.

Wind conditions encountered during the trips varied greatly but were generally favourable. Among all measurements, 70% exhibited positive tailwind components (median tailwind 2.4 m s^{-1} or $0.22 \cdot V_{mp}$, ranging from -10.6 to 18.1 m s^{-1} , i.e. $-0.95 \cdot V_{mp}$ to $1.73 \cdot V_{mp}$). Absolute crosswind strength was typically moderate (median 2.8 m s^{-1} or $0.28 \cdot V_{mp}$) but occasionally large (up to 22.1 m s^{-1} or $2.11 \cdot V_{mp}$). Nonetheless, only 5% of records exhibited crosswinds stronger than $0.5 \cdot V_{mp}$. Tailwinds were significantly higher during migration than during commuting flights ($0.30 \cdot V_{mp}$ vs $0.21 \cdot V_{mp}$, Mann–Whitney–Wilcoxon test $Z=2.56$, $p=0.01$), and crosswind strength significantly weaker, though medians scarcely differed ($0.26 \cdot V_{mp}$ vs $0.28 \cdot V_{mp}$, $Z=-2.99$, $p=0.003$).

In Supplementary material Appendix 1 we estimate the overall flapping fraction using accelerometer data as $f_{fl}=0.927$, and show that there was no significant difference between airspeeds among flapping, flap-gliding and gliding flight modes.

Predicted airspeeds vs wind

Predicted maximum-range airspeed based on full compensation for wind drift (V_{FC}) increased with both headwind and crosswind strength. Figure 1a illustrates contours of maximum-range airspeed in m s^{-1} as a function of tailwind and crosswind for fully compensating gulls which minimize transport costs along the preferred (i.e. goal) direction. For comparison, the wind conditions experienced at each GPS location are indicated by white circles. Maximum-range airspeeds with full drift (V_{GO}) are independent of crosswind, being equivalent to V_{FC} for the same tailwind component and no crosswind (i.e. along the y-axis of Fig. 1a). Figure 1b depicts contours of the percentage difference between V_{FC} and V_{GO} , i.e. $(V_{FC}/V_{GO} - 1) \cdot 100\%$. These differences are typically small ($< 20\%$) in most experienced wind conditions (white circles), but occasionally large ($> 50\%$) in strong crosswinds.

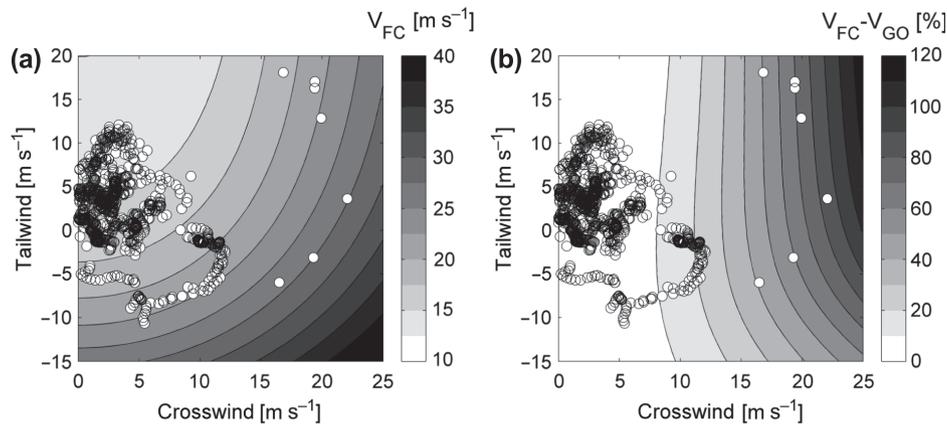


Figure 1. (a) Contours of predicted maximum-range airspeeds (m s^{-1}), modelled after gull FARK (Table 2) flying at 1000 mb and minimizing transport costs along the track direction, as a function of crosswind and tailwind (m s^{-1}), (b) contours of relative deviation (%) between maximum-range speeds of fully compensating (FC) from goal orienting (GO) individuals, otherwise calculated as in (a).

In Supplementary material Appendix 2 we address the effect of various assumptions when analysing the effect of wind on predicted maximum-range airspeeds. We first show that, regardless of wind conditions, predicted maximum-range speeds are similar whether assuming transport costs are minimized along goal directions or along headings. We then show that, to the extent birds allow drift, assuming transport costs are minimized along track directions would result in spurious conclusions regarding the relation between airspeed and wind relative to the goal.

Comparison of measured and predicted flight

Consistent with hypothesis 1, wind conditions had a strong effect on flight altitudes and the extent of experienced wind drift. Birds flew at low altitudes in headwinds and increased their flight altitude especially in combined tailwinds and crosswinds (Fig. 2a). Experienced low-altitude ($< 200 \text{ m}$) tailwinds were stronger during ‘high’ flights (i.e. trips with median flight altitudes $> 200 \text{ m}$) than during ‘low’ flights (trips with median altitudes $< 200 \text{ m}$; Mann–Whitney–Wilcoxon test: $Z=9.96$, $p<10^{-23}$). Low-altitude crosswind strength was actually weaker during high than low flights ($Z=-5.02$, $p<10^{-7}$).

Compensation for drift was highly variable and dependent on tailwind and crosswind strength (Fig. 2b), including over-compensation ($f_c > 1$) and over-drift ($f_c < 0$). Considering measurements pooled from all trips, fractional compensation was higher at flight altitudes below than above 200 m , significantly so in tailwind conditions (median $f_c=1.32$ below vs -0.15 above 200 m , Mann–Whitney–Wilcoxon $Z=-3.8$, $p<0.001$) and marginally so in headwind conditions (median $f_c=0.75$ vs 0.40 , Mann–Whitney–Wilcoxon $p=0.07$, $Z=-1.8$). During trips with median altitudes $> 200 \text{ m}$, fractional compensation was also higher below than above trip median flight altitudes (median $f_c=1.6$ below and 0.5 above median altitudes), but the sample size was small (11 trips) and this difference was not significant (Mann–Whitney–Wilcoxon test, $p=0.11$). Finally, wind direction relative to the coast was significantly related to experienced drift. Fractional compensation in

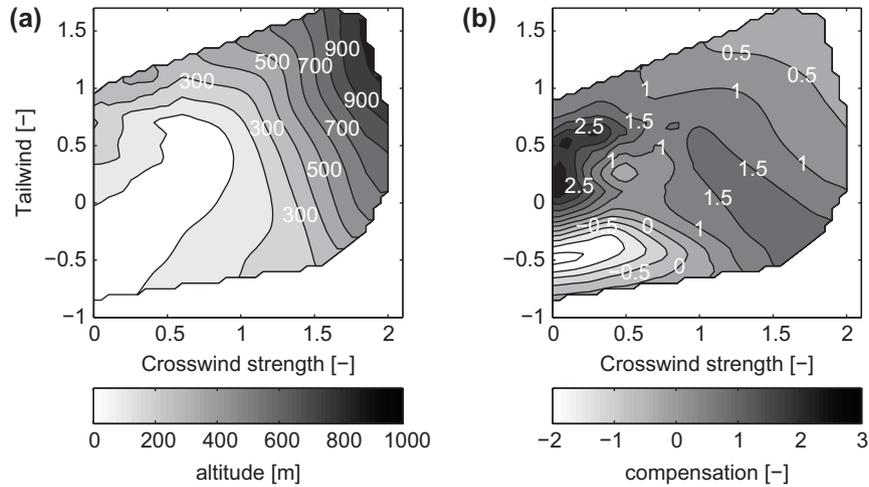


Figure 2. Contours of (a) smoothed altitudes [m] and (b) fractional compensation, f_c , as a function of tailwind component and crosswind strength (both scaled to the minimum power speed, V_{mp}).

onshore winds was significantly lower (median $f_c = 0.52$) than in offshore winds (median $f_c = 1.34$, Mann–Whitney–Wilcoxon test: $Z = 6.3$, $p < 10^{-9}$), indicating enhanced south-eastward drift towards the Dutch coast when winds were favourable for coastal soaring.

The diversity and flexibility in orientation strategy is further illustrated by comparing simulated and actual

trajectories. Figure 3 depicts actual trajectories for six trips (magenta lines) together with predicted trajectories for optimal orientation (OO: cyan lines), full compensation (FC: dotted red lines) and goal orientation (GO: dot-dashed green lines), with wind vectors (grey arrows) depicting wind direction and strength at the simulated pressure level of flight, synchronized with the longitude of actual flight.

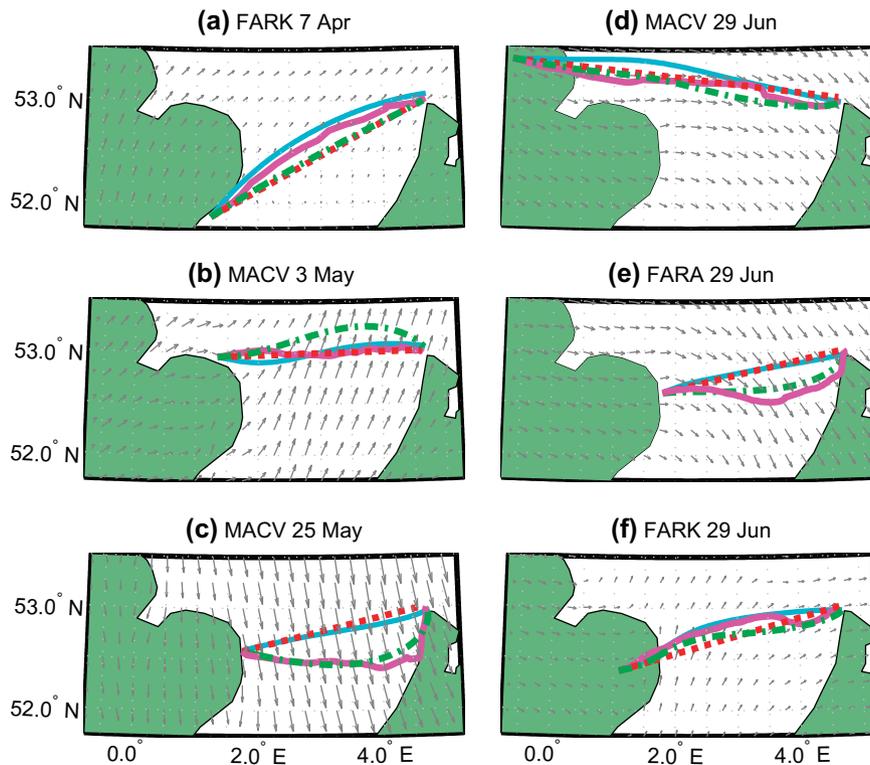


Figure 3. Six trajectories of actual (OO: magenta lines) and simulated gulls flights: optimal orientation (OO: cyan lines), full compensation (FC: dotted red lines) and goal orientation (GO: dot-dashed green lines). Wind vectors (grey arrows) indicate wind speed and direction at the same time as and closest longitude of the actual trajectories, and at the simulated pressure level of flight. Illustrated are (a) trip 20 (maximal wind speed 7 m s^{-1}), (b) trip 6 (maximal wind speed 11 m s^{-1}), (c) trip 8 (maximal wind speed 14 m s^{-1}), (d) trip 10 (maximal wind 9 m s^{-1}), (e) trip 19 (maximal wind 10 m s^{-1}) and (f) trip 21 (maximal wind 7 m s^{-1}). All simulations assumed maximum-range speeds relative to the goal direction.

Individual FARK followed a trajectory approximating OO in a weak low-pressure system on 7 April 2013 (trip 20, Fig. 3a). Such a route is near-optimal for fixed airspeeds (cf. Fig. 2a–b in McLaren et al. 2014), but crosswinds during this trip were weak (maximally 1.9 m s^{-1} i.e. $0.2 \cdot V_{mp}$), so the trajectory did not deviate much from those predicted for other strategies. Individual MACV nearly fully compensated for strong offshore crosswinds from the south (maximally 6.8 m s^{-1} i.e. $0.6 \cdot V_{mp}$) on the night of 3 May (trip 6, Fig. 3b). Contrastingly, this same individual drifted a few weeks later (trip 8 on 25 May, Fig. 3c) in strong onshore crosswinds from the north (maximally 12.1 m s^{-1} i.e. $1.1 \cdot V_{mp}$) and subsequently followed the coast northwards to the breeding colony (50% of accelerometer records along the coast were classified as either gliding or mixed flight). On 29 June, three tagged individuals returned to the colony from England: individual MACV (trip 10), FARA (trip 19) and FARK (trip 21). Individual MACV (Fig. 3d) departed from a more northerly location in England than the other two individuals in moderately favourable winds (median tailwind 3.4 m s^{-1} and crosswind 1.8 m s^{-1}), whereby trajectories differed little between strategies. Individual FARA (Fig. 3e) departed further south in stronger crosswinds (median tailwind 1.7 m s^{-1} and crosswind 4.9 m s^{-1}), allowed considerable drift approximating a GO strategy, and followed the coast thereafter. Individual FARK (Fig. 3f) departed slightly later in the day (17:51 GMT vs 15:16 and 15:51 GMT), chose higher flight altitudes where it experienced favourable winds (median tailwind 4.0 m s^{-1} and crosswind 1.5 m s^{-1}), and initially over-compensated to approximate an OO strategy.

Contrary to hypothesis 2, the birds' estimated headings did not resemble any single strategy. Pooled from all trips, headings were overall closer to optimal orientation (OO), with median deviation 25° and slightly lower in tailwinds (Fig. 4a). Deviations from FC (Fig. 4b) were typically 30° – 40° (median 34°) and even larger in strong headwinds and crosswinds. Median deviation from GO (Fig. 4c) was 43° and especially large in tailwind situations. Within trips, deviations of the strategy most closely approximating measured headings (i.e. with lowest trip-median deviation) ranged from 11° to 44° with a median of 23° (Fig. 4d). Regarding headings (but not necessarily trajectories), ten trips most closely approximated FC, seven trips OO and measured headings were closest to predicted headings for GO in four trips. Diversity in orientation strategy was also evident among individuals, with each strategy (FC, GO and OO) being 'closest' for four different gulls on at least one trip.

Measured airspeeds were, contrary to hypothesis 3, generally much lower than predicted yet varied consistently with hypothesis 3 regarding adjustment to tailwind and crosswind components. Airspeeds were overall only slightly (median 9%) higher than estimated minimum-power airspeed and typically (median 17%) lower than estimated maximum-range airspeeds based on windless conditions. Even in weak winds (wind speeds less than $V_{mp}/4$), airspeeds remained closer to minimum power speeds (median and lower and upper quartiles $1.06 \cdot V_{mp}$, $0.96 \cdot V_{mp}$, $1.17 \cdot V_{mp}$ respectively) than to maximum-range airspeeds excluding wind effects (median and lower and upper quartiles $0.67 \cdot V_{mro}$, $0.61 \cdot V_{mro}$, $0.75 \cdot V_{mro}$ respectively). However, interpolated

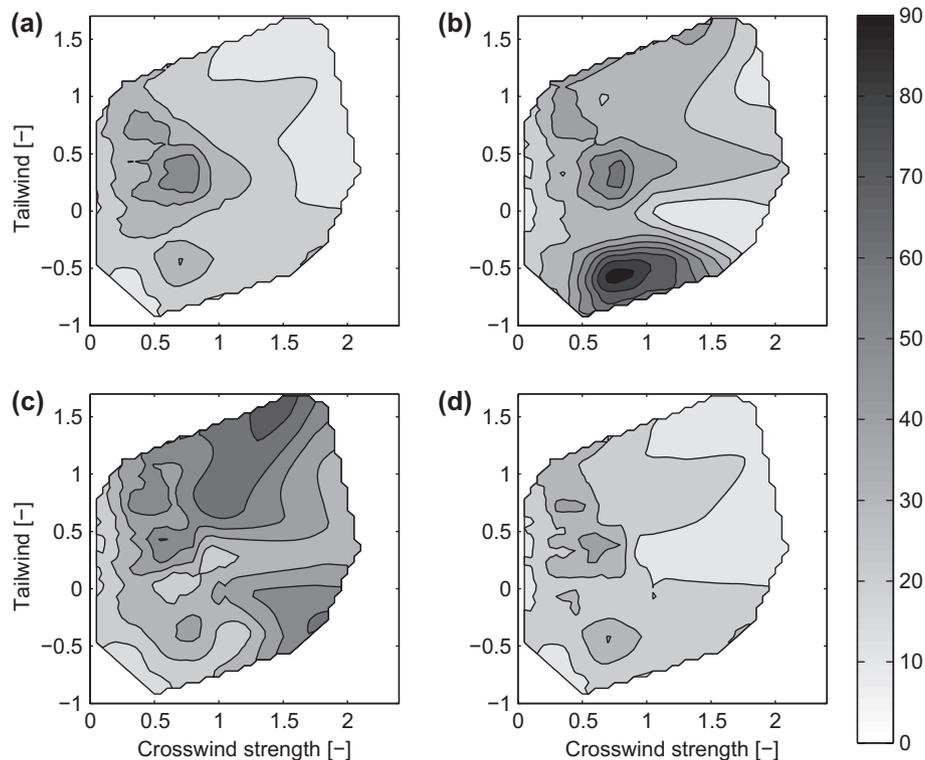


Figure 4. Contour plots of the deviation, in degrees, between predicted and actual angles of heading for all measurements as a function of tailwind and crosswind strength assuming: (a) optimal orientation (OO) using wind-adjusted maximum-range airspeeds, (b) full compensation (FC) for wind drift based on actual airspeeds, (c) goal orientation (GO) based on full drift towards the goal location from the current location and (d) for each trip, the strategy with the lowest median deviation.

contours of measured airspeed relative to V_{mro} (Fig. 5a) show that airspeed exceeded V_{mro} by up to 65% in strong crosswinds and to a lesser extent in headwinds. Figure 5b–d illustrates that airspeed were typically lower than with the wind-adjusted strategies (median among actual measurements 27%, 31% and 27% lower than V_{OO} , V_{FC} and V_{GO} , respectively). Interpolated airspeeds were overall lower than V_{FC} (by 16–44%; Fig. 5b) as opposed to up to 29 and 74% higher than V_{GO} and V_{OO} , respectively (Fig. 5c–d). This difference was consistent among individuals: median airspeeds among individuals was lower than V_{FC} by 14–37% (grand median 27%). We note however that airspeeds in heavy crosswinds were underrepresented overall (Fig. 1a–b).

Gulls were neither as time-efficient nor energy-efficient as predicted to be possible. Figure 6 depicts boxplots of estimated efficiency regarding time expenditure (Fig. 6a) and energy expenditure (Fig. 6b) of actual trips (magenta boxes) and predicted trips (OO: cyan boxes, FC: red boxes and GO: green boxes). Hypothesis 4 (higher energy than time efficiency) was unsupported, with travel efficiencies regarding time expenditure of 0.38–0.88 among trips (median 0.67) and regarding energy expenditure of 0.31–0.90 (median 0.64–0.69, depending on the presumed extent of flapping and gliding flight). This increased flight durations by 0.4–5.8 h (median 1.1 h). Furthermore, efficiency did not differ between migratory and commuting flights regarding

either time expenditure (Mann–Whitney–Wilcoxon test: $Z = -0.29$, $p = 0.77$) or energy expenditure ($Z = -1.20$, $p = 0.23$). Among predicted strategies, those adjusting airspeeds to wind (left-hand boxes in Fig. 6a–b, denoted by ‘var’ on x-axes) were all near-optimally efficient: median efficiency regarding time expenditure (and energy expenditure) was 0.98 (1.00) with OO, 1.00 (1.00) with FC, and 0.97 (0.97) with GO. Compared to measured flights, predicted efficiency of flights based on fixed airspeeds V_{mro} (maximum-range airspeeds of windless conditions, denoted by ‘fix’) were more efficient regarding time expenditure (median efficiency 0.90 with OO, 0.88 with FC and 0.83 with GO, vs 0.67) but were approximately equally energy-efficient (median with OO 0.73, 0.72 with FC and 0.70 with GO, vs 0.64–0.69).

Overall, resultant time and energy efficiency among simulated flights was more strongly impacted by adjustment of maximum range airspeed to wind than by orientation strategy. Median improvements to both time and energy efficiency through orientation differed by 4% among orientation strategies with fixed and 3% among simulations with wind-adjusted airspeeds. Contrastingly, basing simulated flight on wind-adjusted as opposed to fixed maximum-range airspeeds yielded median increases of 12–14% in time efficiency and 37–39% in energy efficiency among the three orientation strategies tested.

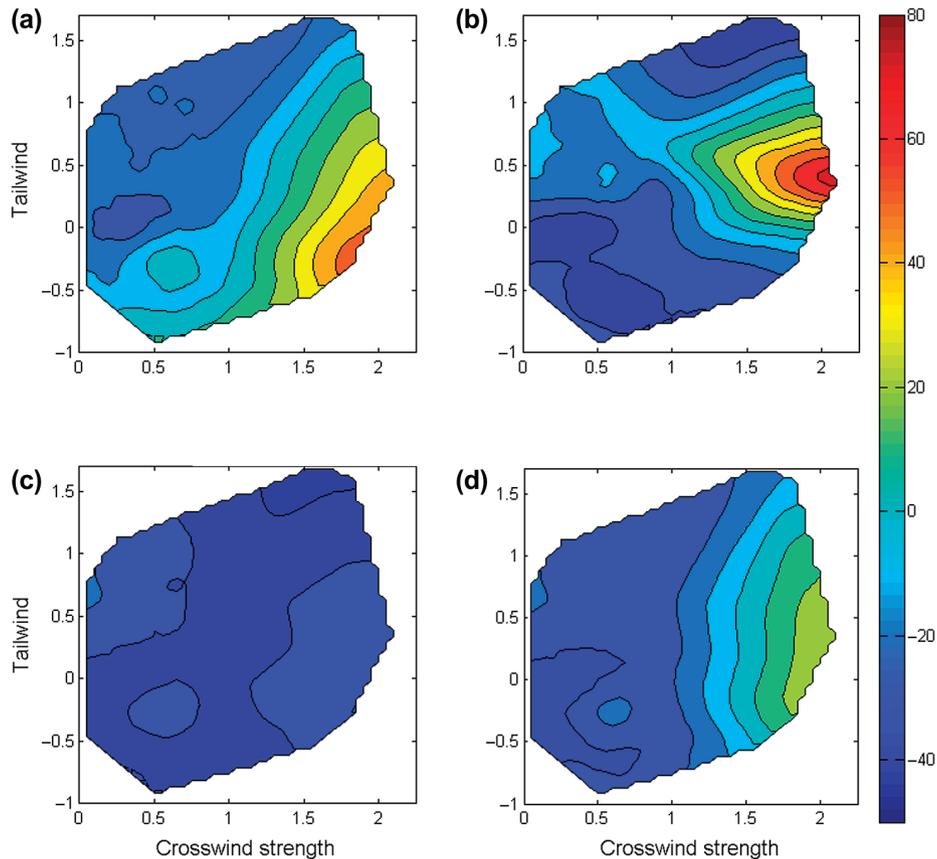


Figure 5. Contour plots of deviation (%) of measured from predicted airspeeds $V_a - V_{mr}$ as a function of tailwind and crosswind strength where predicted airspeed V_{mr} is the maximum-range speed (a) based on windless conditions, i.e. ignoring wind, V_{mro} , (b) based on optimal orientation given fixed airspeeds, V_{OO} , (c) based on full compensation, V_{FC} and (d) based on goal orientation, V_{GO} .

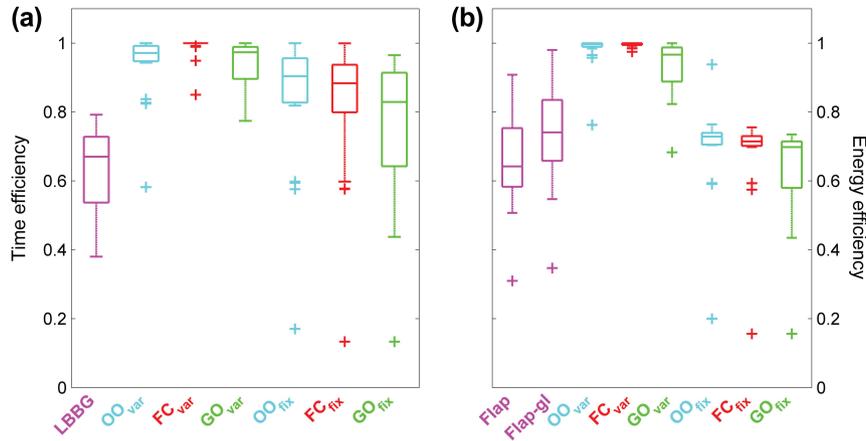


Figure 6. Boxplots of efficiency of (a) time and (b) energy expenditure among all trips as estimated for actual gulls (magenta plots) and simulated trips assuming optimal orientation (OO, cyan boxes), full compensation (FC, red boxes) and goal orientation (GO, green boxes). Estimation of actual energy expenditure in (b) assumed continual flapping flight at minimally the minimum power speed (leftmost box labelled 'Flap') and flap-gliding flight in proportion to the flap/glide ratio from accelerometer data and with slope-soaring (second box from left, labelled 'Flap-gl'). In both (a) and (b), efficiencies are shown for simulated flight involving variable wind-adjusted maximum-range speeds (left-most boxes of simulated trips, labelled 'var') and flight at a fixed airspeed equal to the maximum-range airspeed in windless conditions (right-most boxes of simulated trips, labelled 'fix').

Discussion

The lesser blacked-backed gulls analysed in this study employed primarily flapping flight during these directed flights, but also displayed a remarkable heterogeneity in timing, orientation and apparent urgency to return to their breeding colony. This is consistent with their flexible opportunistic annual routines (Klaassen et al. 2012, Camphuysen 2013), contrasting with those of highly time-constrained long-distance passerine or shorebird migrants (Hedenström et al. 2007, Stanley et al. 2012, Gill et al. 2014).

The role of wind conditions in the decision to depart England is unclear. The relatively higher wind support experienced by the gulls during migration may reflect a heightened reluctance to expend energy during this critical period, even among such flexible opportunists (cf. Klaassen et al. 2012). However, while winds between England and the breeding colony are similar during the spring and summer (Kemp et al. 2010, Supplementary material Appendix 1–3), demonstration of increased wind selectivity during migration would require examining both activity and wind conditions during the days preceding departure.

Wind conditions certainly played a major role in decisions following departure, as summarized in Table 3. As predicted by hypothesis 1, orientation reflected flexible use of high-altitude flight to exploit tailwinds, increased drift in onshore winds to exploit coastal soaring opportunities and

apparent exploitation of combined high- and low-altitude flight to compensate efficiently for lateral drift as proposed by Alerstam (1979b). An ability to gauge wind drift on or near the coast could explain such flexible decision making.

Measured headings did not as per hypothesis 2 closely resemble predicted headings with optimal orientation or any other single orientation strategy (Fig. 4). The extent to which this lack of resemblance stems from uncertainty in wind conditions, altitude variation or use of other flight strategies remains unclear. Nonetheless, flight trajectories variously resembled those resulting from optimal orientation (e.g. Fig. 3a), full compensation (e.g. even at night during trip 6, Fig. 3b and Table 2) and goal orientation (e.g. Fig. 3c). This suggests that discrepancies between measured and predicted headings may have stemmed from alternative strategies or a lack of selective pressure rather than from limitations to navigation. The role of wind in choice of orientation strategy is nonetheless well illustrated by individual MACV's exhibiting on the one hand virtually full compensation in strong 'offshore' winds from the south (Fig. 3b) and on the other hand virtually full drift (goal orientation) in strong 'onshore' winds from the north (Fig. 3c). In the latter case, the landward route provided not only an energetic benefit through coastal soaring, but presumably weaker winds compared to the over-water route due to increased surface friction over land. Drifting seaward in winds from the south would have provided neither of these benefits, and

Table 3. Overview of main results from this study.

Research question	Result
Hypothesis 1: enhanced drift (a) at high altitudes and (b) in onshore winds	(a) Y (b) Y
Hypothesis 2: headings resemble (near) time-optimal orientation	N
Hypothesis 3: airspeeds (a) approach or exceed maximum-range speeds and increase in (b) headwinds and (c) crosswinds	(a) N, (b) Y, (c) Y
Hypothesis 4: prioritization of minimizing energy expenditure over time expenditure in flight	N
Airspeed adjustments offer potentially more/less energy savings than orientation strategies	more
Analysing airspeed adjustments relative to track as opposed to goal directions leads to spurious interpretation (pseudo-compensation)	Y

moreover brought most gulls outside of their general home range (Camphuysen et al. 2015).

As predicted by hypothesis 3, the gulls were shown to adjust their airspeed flexibly at sea to experienced tailwind and crosswind. These adjustments were similar to those expected when minimizing transport costs and fully compensating for wind drift (Fig. 5c), suggesting highly-developed adaptation of flight to wind. Our study therefore provides evidence that when crosswinds can be defined unambiguously, adaptive adjustment of airspeed to both tailwind and crosswind components is feasible (cf. Hedenström et al. 2002, Karlsson et al. 2010b, Yoda et al. 2012, Sapir et al. 2014b). However, contrary to hypothesis 4, airspeeds were nearly ubiquitously lower than predicted, resulting in low estimated efficiency of time and energy expenditure (Fig. 6). Note that the gulls' efficiencies were if anything over-estimated considering that simulations did not incorporate flight altitude selectivity or potential gains from (flap-) gliding flight and coastal soaring. Hence, even when accounting for the sources of uncertainty from previous studies (parameterization of aerodynamic models, uncertainty of crosswind, orientation or foraging effects), our study supports the notion that airspeeds in goal-directed flight can result from a trade-off between minimizing instantaneous power and transport costs (cf. Schnell and Hellack 1979).

Nonetheless, given the extent and directedness of the flights and the gulls' evident ability to gauge and react to wind, it is somewhat surprising that, contrary to hypotheses 3 and 4, they did not further reduce their flight costs by flying faster. Possible behavioural explanations for the lower airspeeds include 1) a vigilant strategy to save energy for e.g. unanticipated weather, spontaneous feeding opportunities or confrontations with other birds at sea, 2) reduced time and energy constraints among non-breeders (Velando et al. 2010, Shamoun-Baranes et al. 2011, Camphuysen 2013) or 3) given that (fly-) foraging trips occur more frequently than extended goal-directed flights among these gulls (Camphuysen 2013), a lack of selective pressure to fully exploit modulation of airspeed to wind during extended flight in order to minimize transport costs (Rayner 1988). However, it cannot be excluded that the over-predicted airspeeds may reflect aerodynamic models currently underestimating the required power for flight, at least for this species (cf. Muijres et al. 2012, Pennycuick et al. 2013). Given the strong evidence that gulls reduced transport costs adaptively by adjusting flight to wind (e.g. Fig. 2a, 3 and 5), their apparent disregard for transport costs in weak winds (i.e. flying much closer to V_{mp} than V_{mro}) may instead indicate their airspeeds being over-predicted.

Other factors seem unlikely to fully account for the discrepancy in this study between measured and predicted airspeeds. Physiological limitations to efficient flight at higher airspeeds e.g. a fixed-gear hypothesis (Thomas and Hedenström 1998, Muijres et al. 2011) could be partly responsible but airspeeds were also over-predicted in near-windless conditions (Fig. 5). All of the trips presumably preceded wing moult (Camphuysen 2013), which could have reduced both their incentive to expend energy and their flight efficiency (Hedenström and Sunada 1999). Despite the loggers plus harnesses weighing only 2.1–3.1% of weight at capture,

there remains a chance that the 'handicap' of wearing the loggers reduced incentive to expend energy (Vandenabeele et al. 2012, Elliott et al. 2014b, Hupp et al. 2015). However, simulations assuming doubled body drag still over-predicted airspeeds (Supplementary material Appendix 3). The fact that airspeeds appeared overall lower than predicted rather than both over- and under-predicted (cf. Fig. 5c) presumably excludes such factors as the birds' limitations in gauging or predicting wind conditions at sea, or modelling errors arising from estimated wing morphology (Supplementary material Appendix 3), wind or altitude data. Using instantaneous as opposed to next-location ground speed estimates excludes sinuosity being a factor, supported by the fact that trajectories generally exhibited low sinuosity. Finally, it seems unlikely that misdiagnosed flight modes strongly influenced results, given that non-flapping flight was uncommon and involved similar airspeeds to flapping flight (Supplementary material Appendix 1).

The sensitivity of predicted maximum-range airspeeds to orientation strategy (Fig. 1 and Supplementary material Appendix 2) illustrates that, if possible, it is preferable to analyse reaction to wind relative to goal directions or headings rather than travel i.e. track directions. A potential pitfall in analysing reaction to wind relative to track directions is that tailwind and crosswind components become convoluted if drift is significant, which may obscure actual adjustments to wind (cf. Hedenström et al. 2002, Mateos-Rodríguez and Liechti 2012, Safi et al. 2013, Elliott et al. 2014a, Horton et al. 2014, Mitchell et al. 2015). Hence in addition to the well-documented issue of pseudo-drift (mistaking heterogeneity in preferred directions for tolerance of wind drift; Alerstam 1978, 2011), analysing reaction to wind can also be confounded by pseudo-compensation, i.e. mistaking track directions for preferred headings when individuals are partially or fully drifted by the wind. A second issue, which we avoided by selecting inbound flights, is whether outbound trips are truly goal-oriented or are partly chosen to benefit total flight costs over both legs of the journey. Interestingly, the foraging flights by fructivorous bats analysed by Sapir et al. (2014b) often exhibited extended drift on outbound journeys resulting in higher wind support on the return. While the bats' foraging locations remained consistent, analysis of round-trip flights should more generally also account for wind selectivity in the context of available goal locations.

While tracking technology has been available for many decades (Cochran et al. 1967), using accelerometers (Gleiss et al. 2011, Spivey and Bishop 2013, Portugal et al. 2014) or alternatively combined heart-beat and wingbeat measurements (Weimerskirch et al. 2001, Sapir et al. 2010) provide an exciting opportunity to assess energy expenditure remotely. In this study we estimated energy expenditure using an aerodynamic model together with a flapping ratio estimated from accelerometer data. Ongoing research on energetics of intermittent flight (Lentink et al. 2010, Muijres et al. 2012) may soon provide better estimates of energy expenditure and insight into flight strategies in variable wind scenarios.

In conclusion, while these gulls displayed highly adapted reaction to wind during extended goal-directed flight at sea, they apparently prioritized neither time nor energy expenditure during flight (cf. Klaassen et al. 2012). This implies

that the currency of movement used to assess optimal flight behaviour in extended flight can go beyond a single trip or efficiency related costs (cf. Hedenström and Ålerstam 1995, 1997), for example through being adapted to maintain lower airspeeds beneficial to fly-foraging. However, we cannot rule out that flight costs among these birds are higher than currently supposed (cf. Muijres et al. 2012, Pennycuik et al. 2013). It may well be that among more highly time-constrained taxa (e.g. long-distance migrants), adjustment of airspeed to wind may more closely approach optimal predictions. Clearly, volant animals have many ways of adapting to and negotiating winds, but hierarchies between driving factors and constraints to adaptation remain unresolved.

Acknowledgements – These studies are part of a long-term demographical and ecological study on sympatric breeding gulls by the Royal Netherlands Inst. for Sea Research (NIOZ) at Texel. Model simulations were facilitated by the Netherlands eScience Center (<<http://esciencecenter.com>>), project 660.011.305, and BiG Grid infrastructure for e-science (<www.biggrid.nl>). We are grateful to all who skilfully assisted with fieldwork, to Edwin Baaij for technical support with UvA-BiTS, and to Thomas Ålerstam and Heiko Schmaljohann for helpful comments and constructive suggestions.

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Supplementary material (Appendix JAV-00828 at <www.avianbiology.org/appendix/jav-00828>). Appendix 1–3.