Flexible flight response to challenging wind conditions in a commuting Antarctic seabird: do you catch the drift?

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Flight is intrinsically an energetically costly way of moving and birds have developed morphological, physiological and behavioural adaptations to minimize these costs. Central-place foraging seabirds commute regularly between nesting and foraging areas, providing us with opportunities to investigate their behavioural response to environmental conditions that may affect flight, such as wind. Here we tested hypotheses on how wind conditions influence flight behaviour in situations devoid of the confounding effect that, for instance, active foraging behaviour can have on movement patterns. We studied the Antarctic petrel, *Thalassoica antarctica*, a seabird breeding far inland in Antarctica and commuting through vast ice-covered areas characterized by steady and strong winds as well as a strict absence of foraging opportunities. We combined the three-dimensional location data from 79 GPS tracks with atmospheric wind data over three consecutive breeding seasons (2011−2013) in order to assess individual flight responses to wind conditions. Antarctic petrels encountered generally unfavourable winds, particularly during return flights. Despite their capacity to adjust their speed and heading in order to maintain constant track direction (compensation) in the strongest winds, they generally drifted as wind strengthened. Strong winds induced low-altitude flight. Birds tended to otherwise fly relatively high, but at altitudes with more favourable winds than what they would have encountered if flying higher. Our results show that commuting Antarctic petrels: (1) can tolerate a certain amount of drift according to wind conditions and (2) might be more limited by their ability to assess drift, rather than compensate for it, at least during returning flights.
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The movements of individuals are linked to key processes such as foraging, dispersal, migration or reproduction that ultimately influence the dynamics of animal populations across many taxa (Chapman et al., 2011). While the benefits of extensive mobility are obvious, they come at important energetic costs, especially for flying animals (Bale, Hao, Bhalla, & Patankar, 2014). Active flight is among the movement modes generating the highest levels of energy expenditure (Elliott et al., 2013; Pennycuick, 1975; Tucker & Schmidt-Koenig, 1971) and long-ranging birds have evolved morphological, physiological and behavioural adaptations to minimize these costs (Maina, 2000; Norberg, 1995; Portugal et al., 2014; Weimerskirch, Martin, Clerquin, Alexandre, & Jiraskova, 2001). During long trips, such as migration or long-range foraging, energy expenditure has to be minimized while maximizing transport efficiency (e.g. migration speed; Liechti, 2006; Kemp, Shamoun-Baranes, Van Gasteren, Bouten & Van Loon, 2010; Vansteelant et al., 2015) or simply the probability of reaching

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the goal (Bulte et al., 2014). The energetic costs of flight depend on environmental conditions, in particular wind (Elliott et al., 2014; Tucker & Schmidt-Koenig, 1971). Birds have therefore been predicted to adapt their behaviour to wind conditions so as to minimize flight costs (Amélineau et al., 2014; Karlsson, Henningsson, Bäckman, Hedenström, & Alerstam, 2010; Klaassen, Hake, Strandberg, & Alerstam, 2010). How flying birds respond to wind conditions will vary depending on whether they are travelling, thus trying to minimize travel time or costs, or foraging (i.e. actively searching for food), thus also trying to maximize energy income. The flight pattern of an actively foraging bird is therefore influenced not only by winds but also to a large extent by resource distribution (Fauchald & Tveraa, 2006). This makes the interpretation of the influence of wind conditions on the observed flight patterns more complex (Louzao, Wiegand, Bartumeus, & Weimerskirch, 2014; Raymond et al., 2010), particularly because wind and resource distribution can interact and affect movement patterns differently depending on the spatial scale considered (Fritz, Said, & Weimerskirch, 2003). Study systems that allow the testing of hypotheses on the influence of wind conditions on bird flight without confounding effects potentially induced by foraging behaviour should hence prove very valuable. One example of such a system is the commute by central-place foragers between their feeding areas and the central delivery point, usually a breeding site (Elliott et al., 2014; Niizuma et al., 2001; Norberg, 1981).

Here, we focused on the flight response of a commuting seabird, the Antarctic petrel, *Thalassoica antarctica*, that breeds on the Antarctic continent, one of the windiest places on Earth (Turner et al., 2009). Large breeding colonies are found in mountain slopes situated several hundreds of kilometres away from the nearest open water and at altitudes up to 1600 m above sea level (van Franeker, Gavrilo, Mehlum, Veit, & Woehler, 1999). To our knowledge, no other flying seabirds, apart from the sympatric snow petrel, *Pagodroma nivea*, use nesting sites separated from the nearest potential foraging area by such an extent of habitat that is absolutely unsuitable for foraging. Consequently, Antarctic petrels cover long distances over continental ice when commuting between their colony and their feeding areas at sea. One can realistically assume that a commuting Antarctic petrel aims at flying as directly as possible to foraging areas on its outbound flight, or to the breeding colony on its inbound flight. This is a situation that is broadly similar to that encountered by terrestrial birds during transoceanic migrations (Bulte et al., 2014), although at a smaller spatiotemporal scale. Commuting birds are, however, strongly constrained by the necessity to limit the duration of their foraging trips (e.g. to maintain high frequency of chick provisioning; Tveraa, Lorensten, & Sæther, 1997; Houston, 2006). Time spent travelling and the associated flight costs can indeed affect the net energy gain over a given foraging trip, with potential fitness consequences (Elliott et al., 2014; Norberg, 1981).

For given wind conditions, different flight tactics may thus be associated with different fitness costs and benefits. It is critical for species living in areas with strong and persistent winds, such as Antarctica, to have the ability to take advantage of favourable wind conditions or mitigate unfavourable ones (Weimerskirch, Chastel, Barbraud, & Tostain, 2003; Weimerskirch et al., 2014), and strong behavioural responses to wind conditions are expected to have evolved (Spear & Ainley, 1997a). Our main objective was to determine the extent to which commuting Antarctic petrels can compensate for unfavourable wind conditions, i.e. adjust their heading and airspeed to maintain constant track direction (Karlsson et al., 2010; Liechti, 2006; McLaren, Shamoun-Baranes, Dokter, Klaassen, & Bouten, 2014). We tested the hypothesis that different constraints at departure versus return should elicit contrasting responses to wind conditions. Departing birds should

tolerate drifting from their preferred direction when leaving their colony (Prediction 1), as they are not constrained by the necessity to reach a specific location, as shown by the huge areas covered at sea by foraging Antarctic petrels (Fauchald & Tveraa, 2003). Returning birds, however, must reach the exact location of their breeding colony. We thus predicted that they would minimize the travelling distance back to their nest by reducing the amount of drift during return flights and showing stronger compensation for unfavourable winds (Prediction 2). Finally, we predicted that Antarctic petrels would select cruising altitudes where wind conditions are more favourable, i.e. with weaker wind or tail wind, thereby minimizing the need for compensation (Prediction 3).

METHODS

Study Site and Species

Our study took place at the Svarthamaren breeding colony (71°53′S, 5°10′E) in Dronning Maud Land, Antarctica, from December to February during three breeding seasons (2011−2012 to 2013−2014). The colony of about 200 000 breeding pairs (Descamps, Tarroux, Varpe, et al., 2015) is located at 1600 m above sea level (asl) and 184 km from the nearest potentially open water, at the limit of the Antarctic ice shelf (Fig. 1). The Antarctic petrel is a medium-sized fulmarine petrel that weighs ca. 600 g. Females lay a single egg at the end of November/early December and hatching occurs in mid-January (Descamps, Tarroux, Lorentsen, et al., 2015). Both parents incubate the egg and guard and feed the chick until fledging in March. They alternate incubating shifts and foraging trips, the duration of which decreases throughout the season (Lorentsen & Røv, 1995; Varpe, Tveraa, & Folstad, 2004).

Ethical Note

All capture and handling procedures were in accordance with the permits provided by the Norwegian Animal Research Authority (NARA/FDU permits no. 3714 and 5746). Breeding birds were captured on their nest by hand during the incubation or chick-rearing periods. We outfitted 131 individuals with a miniaturized GPS unit (CatTraQ, Catnip Technologies Ltd., U.S.A., catniptech.com). The original plastic casing of each GPS unit was removed at the Institut Pluridisciplinaire Hubert Curien (CNRS, Strasbourg, France). We added a waterproof heat-shrinking tube casing for a final weight of ca. 20 g. The customized units were then taped to the base of the two central rectrices using black Tesa tape (Appendix Figs. A1, A2). We did not observe any obvious disturbance of the behaviour or flying abilities. We recaptured birds upon return from their foraging trip and avoided outfitting the same individual more than once per breeding season, although on six occasions birds could not be recaptured before they left for a second foraging trip, and one bird was mistakenly equipped twice in the same breeding season (details in Appendix Table A1). We did not find any significant short-term effect of GPS units on the average breeding success of GPS versus non-GPS birds (logistic regression: $z = 1.279$, $P = 0.201$, $N = 1142$). Pooling all years, the average survival probability was 13.7% (95% CI = [7.8; 19.7]; $N = 131$) and 18.3% (95% CI = [15.9; 20.7]; $N = 1011$), respectively, for GPS and non-GPS birds.

GPS Data and Flight Track Parameters

To ensure that battery duration would cover the longer trips at the beginning of the breeding season, we programmed GPS units to record locations at different intervals throughout the season: 90 min ($N = 1$), 60 min ($N = 1$), 30 min ($N = 19$), 10 min ($N = 37$) and 5 min ($N = 21$) intervals. To test for potential effects of
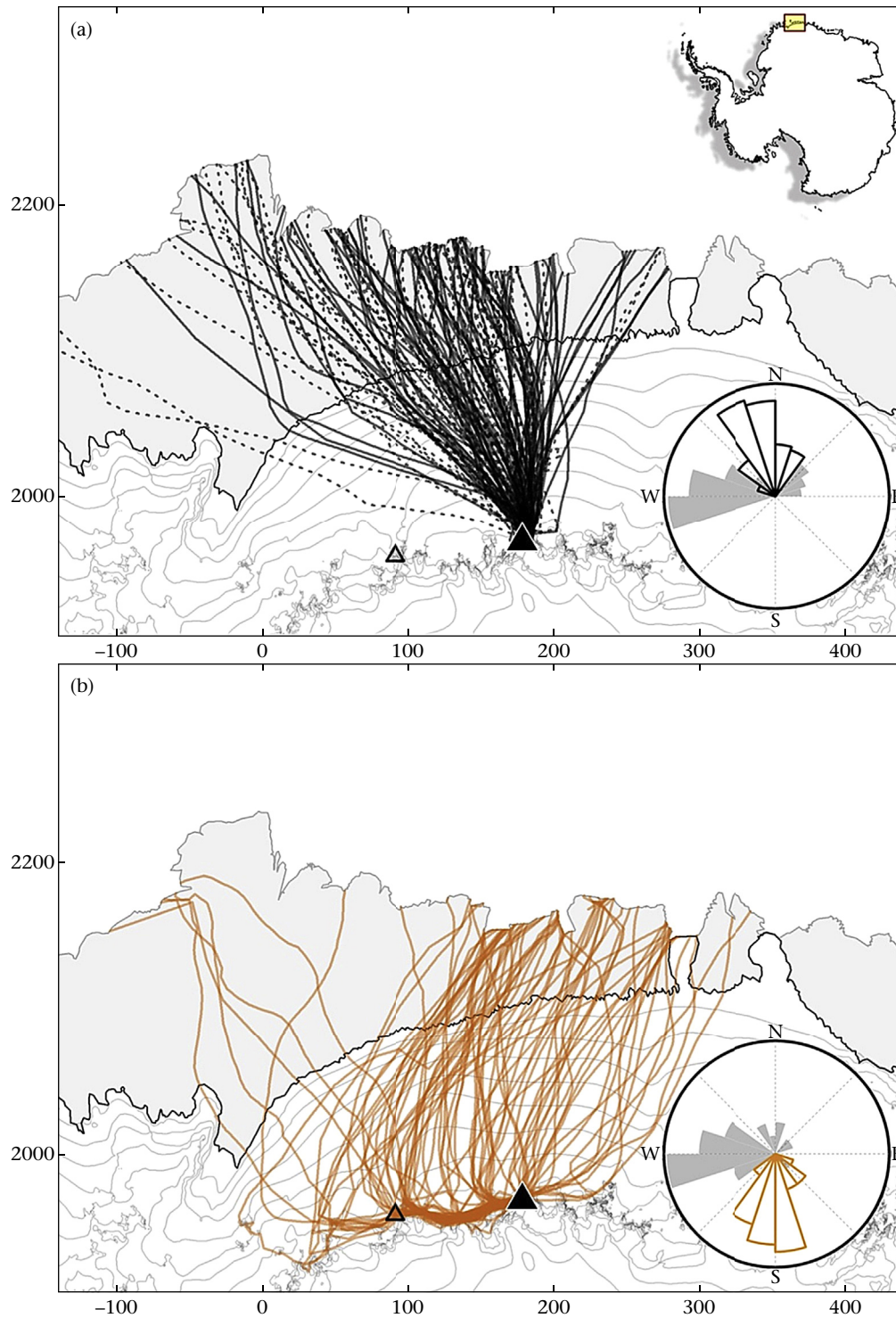
Figure 1. (a) Departure and (b) return sections of 79 Antarctic petrel GPS flight tracks recorded during three breeding seasons in Dronning Maud Land, Antarctica. Dashed lines represent the additional tracks ($N = 58$) that were not included in analyses because the GPS unit failed before birds returned. Locations of the study breeding colony (Svarthamaren [71°53′S, 5°10′E]; filled triangle) and the neighbouring colony (Jutulsessen [72°03′S, 2°41′E]; empty triangle) are indicated. Elevation contour lines are separated by 200 m. Rose diagrams show the frequency distributions of wind blowing directions (shaded sections) and bird track directions (empty sections). Map projection is Polar Stereographic.

sampling interval on GPS speed measurements, we rediscretized all tracks at 90 min intervals and compared the speed measured for those tracks to the original ones (only for GPS units programmed at 30 min or less; $N = 154$ sections). We detected a small but statistically significant effect of the GPS sampling interval (mean difference + SE = $-0.46 + 0.09$ m/s; paired t test: $t_{153} = 5.0802$, $P < 0.001$). Because this difference represents <4% of the average speed measurements, and since only 3% of our GPS units were programmed at intervals ≥ 60 min, it is highly unlikely that this could have affected our results. Location data were downloaded from the GPS units and projected in Polar Stereographic projection with 70°S as standard parallel. Each track was speed-filtered using

stepwise recursive routines excluding all locations generating unrealistic ground speed values, using a conservative threshold of 40 m/s based on ground speed measurements on Procellariiformes of similar size and made in varying wind conditions (Spear & Ainley, 1997b). Land and ice shelf contours were obtained from the Mosaic Of Antarctica dataset (Scambos, Haran, Fahnestock, Painter, & Bohlander, 2007). All flying heights are expressed in metres above ground level, unless otherwise indicated. To determine flying height for each location, the ground level was estimated based on the Radarsat Antarctic Mapping Project Digital Elevation Model (hereafter DEM; Liu, Jezek, & Li, 1999) and then subtracted from the GPS-recorded altitude. We tested for the altitudinal accuracy of our GPS units by collecting positions from a location of known altitude within the breeding colony. We programmed three units at 5 min intervals during ca. 4.5 h each and obtained a total of 166 GPS fixes. The mean absolute altitudinal error was 52 m (95% CI = [24; 79]), i.e. well within the resolution of the wind data (see below). The data used in this study are available on Movebank (www.movebank.org, Movebank ID 121041109) and are published in the Movebank Data Repository with http://dx.doi.org/10.5441/001/1.q206rm6b (Tarroux et al., 2015).

Only locations situated above the Antarctic continent (ice cap) or ice shelf, i.e. where foraging is impossible, were selected for analysis. Numerous polynyas are situated along the ice shelf around Antarctica (Nihashi & Ohshima, 2015), and constitute very productive and potentially attractive foraging areas (La et al., 2015; Stirling, 1997). Thus, all locations situated farther than the ice shelf were not considered, as they could correspond to active foraging behaviour. Only 129 GPS units (for a total of 7058 locations) had usable data. We split all tracks into a departure and a return section, and only tracks for which both sections were available (N = 79 trips; 4687 locations) were used in analyses to allow for paired comparisons (Fig. 1 and Appendix Table A1). At departure, Antarctic petrels sometimes soar above or within ca. 2 km from the colony, in order to take advantage of orographic and thermal winds that are generated above the scree slopes (Mehlum, Gjessing, Haftorn, & Bech, 1988; A. Tarroux, H. Weimerskirch, Y. Cherel & S. Descamps, personal observations), which could lead to spurious relationships between estimated near-zero ground speed values and wind velocity. A conservative threshold of 4 km from the colony was thus used to exclude those locations. Owing to imprecision in both GPS and DEM altitudinal values, 526 locations (7.5%) were situated below the DEM-defined ground level: in these cases, all locations were shifted to 10 m, thereby assuming that birds were flying close to ground level in those instances. The following parameters were calculated for the departure and return section of each trip: travel time, total distance covered, track direction and straight-line distance between the colony and the farthest location for a given section (i.e. at the ice shelf boundary; Appendix Table A1).

Wind Data Extraction and Interpolation

Wind data were extracted from the Antarctic Mesoscale Prediction System (AMPS), a model system run by the Mesoscale and Microscale Meteorology (MMM) Division of the National Center for Atmospheric Research (NCAR) and dedicated to real-time numerical weather prediction in Antarctica (Powers, Manning, Bromwich, Cassano, & Cayette, 2012; Powers et al., 2003). It is a collaborative effort between NCAR's MMM group and The Ohio State University (OSU). The AMPS uses the Polar WRF, a version of the Weather Research and Forecasting Model (WRF) optimized for polar environments and developed by the Polar Meteorology Group at OSU. It performs forecasts twice a day at 0000 and 1200 UTC for all of Antarctica. For each AMPS forecast, the first 12 h were discarded as the model adjusted to the Antarctic environment, then wind outputs at 3 h intervals from forecast hours 12 to 24 were extracted. Because forecast winds are used, it is assumed that these closely match actual conditions, as has been verified by forecast performance studies of Polar WRF (Bromwich, Otieno, Hines, Manning, & Shilo, 2013). Owing to a change in wind model spatial resolution in 2012, the resolution was 15 km in 2011–2012 and 10 km in the two subsequent seasons (Powers et al., 2012).

To determine the wind conditions at the birds' locations, we first grouped the timestamps of all GPS locations into 3 h bins, based on
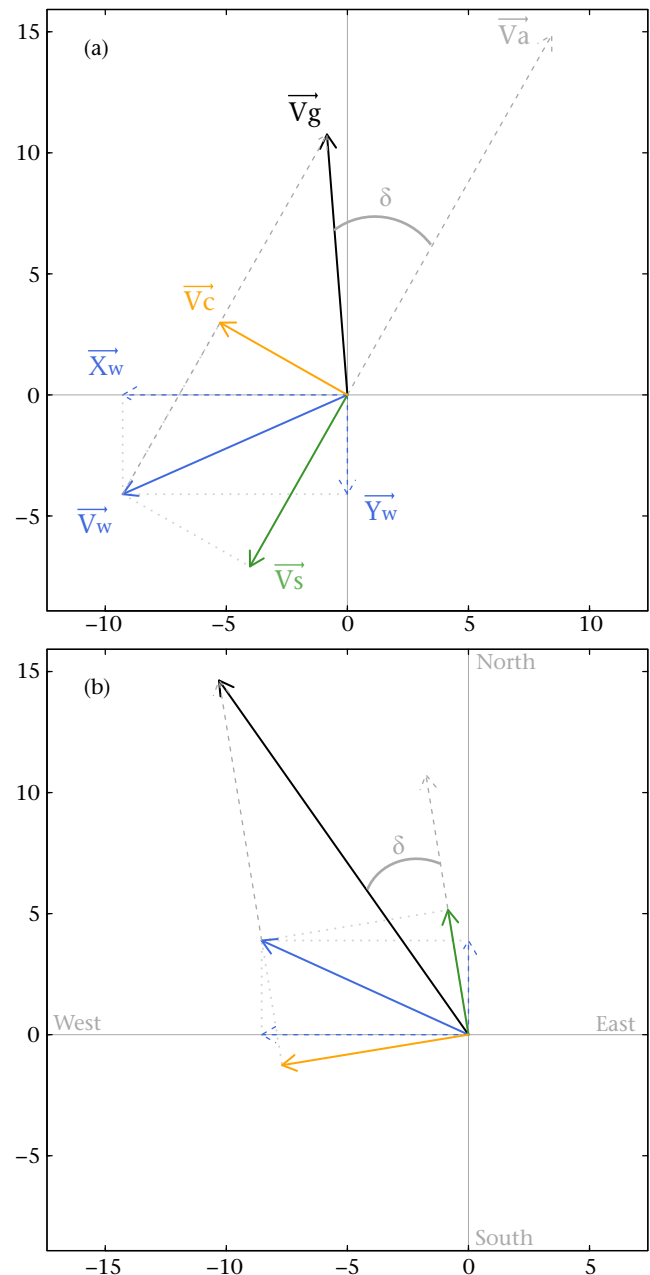

Figure 2. Graphic representation of the vectors used in analyses (Table 1), in two cases drawn from our dataset: a bird flying with (a) head wind, i.e. 'negative wind support' or (b) tail wind. The bird displacement vector is $\overrightarrow{Vg}$ (ground velocity, black arrow); the wind vector is $\overrightarrow{Vw}$ (wind speed; blue arrow) and can be decomposed into a zonal component ($\overrightarrow{Xw}$; horizontal dashed blue arrow) and a meridional component ($\overrightarrow{Yw}$; vertical dashed blue arrow); the airspeed vector is $\overrightarrow{Va}$ (dashed grey arrow); the wind support component is $\overrightarrow{Vs}$ (i.e. the projection of $\overrightarrow{Vw}$ on $\overrightarrow{Va}$; green arrow); the cross-wind component is $\overrightarrow{Vc}$ (i.e. the projection of $\overrightarrow{Vw}$ on the perpendicular to $\overrightarrow{Va}$; orange arrow). Units on both axes are in m/s.

model forecast times $\pm$ 1.5 h. Then the corresponding model data were interpolated from the four surrounding grid cells associated with each bird location and altitude. Each location was thus characterized by a zonal or west-east (hereafter Xw) and a meridional or south-north (hereafter Yw) wind component. If model altitude was higher at any of the surrounding grid points than the reported GPS altitude, meaning the bird flew 'below' the lowest level of the model grid at that instance, the interpolated wind data at those grid points were noted as missing. The final wind data for each of the birds' locations were averaged based on the remaining (non-missing) grid points. To obtain wind conditions below and above the birds' locations (wind profiles), wind data were interpolated at every 200 m altitude level, from ground level up to an altitude of 4000 m above mean sea level at each GPS location.

Vector Calculations and Definitions Used

Based on the GPS and wind data, a series of vectors were calculated to determine: (1) the wind speed and direction (wind velocity or $\vec{Vw}$) both at flight height and above or below flight height; (2) the bird's displacement relative to the ground (ground velocity or $\vec{Vg}$). Wind direction is defined here as the direction the wind is blowing to, for easier comparison with the direction of bird flight (Shamoun-Baranes, van Loon, Liechti, & Bouten, 2007). Wind velocity can be decomposed into two perpendicular vectors, corresponding to the Xw ($\vec{Xw}$) and the Yw ($\vec{Yw}$) components mentioned above (Fig. 2). Based on these, the following components were calculated (summarized in Table 1).

(1) The airspeed ($\vec{Va}$) characterizes the bird's displacement relative to the air flow such that $\vec{Va} + \vec{Vw} = \vec{Vg}$ (Liechti, 2006; Shamoun-Baranes et al., 2007). In other words, the direction of $\vec{Va}$ indicates the bird's heading, while the direction of $\vec{Vg}$ indicates the direction of the ground track.

(2) The wind support ($\vec{Vs}$) is the projection of $\vec{Vw}$ on $\vec{Va}$. Vs can take positive (tail wind) or negative (head wind) values and corresponds to the relative wind that the bird actually experiences.

(3) The cross wind ($\vec{Vc}$) is the projection of $\vec{Vw}$ on the perpendicular to $\vec{Va}$. Vc can take positive (blowing to the right of the bird heading) or negative (blowing to the left) values.

(4) The angular difference (δ) is the angle between the ground velocity $\vec{Vg}$ and the bird's heading (or airspeed, $\vec{Va}$) that was used when estimating magnitude of drift versus compensation (see below).

(5) The difference in zonal wind component (ΔXw) at a bird's flying height versus above was calculated as follows: $\Delta Xw = Xw_i - mean(Xw_{i+1}, Xw_{i+2})$, where Xw_i is the zonal wind component at the bird's altitude and Xw_{i+1} and Xw_{i+2} are the values for this component one and two levels (i.e. 200 m and 400 m) above the bird's flying height, respectively. The same

equation was used to calculate ΔXw below the bird's flying height, as well as for the difference in the meridional wind component (ΔYw), also above and below the bird's flying height.

Statistical Analyses

All data processing and calculations were conducted in R 3.1.1 (R Development Core Team, 2015). Package proj4 v.1.0—8 (Urbanek, 2012) was used for the projection of GPS coordinates and map layers (Antarctic continent and ice shelf boundary) and package adehabitatLT v.0.3.16 (Calenge, 2006) was used for the calculation of basic track parameters (step length, time interval, relative angle, track direction) and for rediscretizing the tracks. Paired *t* tests were run in order to compare wind conditions and flight track parameters at departure versus return. Means and standard deviations of angular directions were calculated using circular statistics (Batschelet, 1981) and the package circular v.0.4—7 (Agostinelli & Lund, 2013). Package mgcv v.1.8—3 (Wood, 2011) was used to run additive models (Wood, 2006; Zuur, Saveliev, & Ieno, 2014) when testing for the effects of wind conditions on flight parameters. To compensate for different GPS fix intervals and deal with autocorrelation in our data, all data were averaged per section and per individual in all models and paired *t* tests. The relative magnitude of drift versus compensation was estimated by regressing the ground track direction γ on the angular difference δ (see above) in order to estimate the slope *b* of the linear relationship (method 1 in Green & Alerstam, 2002). A value of $b = 0$ means full compensation (heading is adjusted to maintain a constant ground track direction) and $b = 1$ means full drift. Birds started their return journey to the colony from different locations, and therefore had different 'directions to destination' (sensu Green & Alerstam, 2002). This prevented us from estimating the average magnitude of drift and a preferred direction at return. We could, however, estimate the straightness of the return flight to the colony by calculating the ratio D_c/D_s, where D_c is the actual ground distance covered by the bird and D_s is the straight line between the first location of the return section and the breeding colony.

RESULTS

A total of 79 foraging trips (75 individuals) representing 4687 locations were analysed. For any section (departure or return), flight duration ranged from 2.6 to 14.7 h and ground distance covered ranged from 187 to 646 km (Table 2). Previous studies at the same site (Lorentsen & Røv, 1995) and our own field observations suggest the occurrence of a minimum of 12 foraging trips per breeding season for each mate of a successful breeding pair. Based on the average ground distance birds covered while commuting to and from their foraging sites (this study), this translates into a cumulated 6400 km of active flight over land/ice shelf per breeding

Table 1
Nomenclature of vectors and associated parameters used in the calculations and figures

δ	Angular difference between the ground track ($\vec{Vg}$) and the bird's heading, i.e. airspeed, ($\vec{Va}$)
γ	Ground track direction (relative to geographical north)
$\vec{Va}$	Bird's airspeed (displacement in the air flow), the direction of which corresponds to the bird's heading
$\vec{Vc}$	Cross-wind component (projection of $\vec{Vw}$ on the perpendicular to $\vec{Va}$)
$\vec{Vg}$	Bird's ground velocity or ground speed
$\vec{Vs}$	Wind support component (projection of $\vec{Vw}$ on $\vec{Va}$)
$\vec{Vw}$	Wind velocity (i.e. wind speed and direction)
$\vec{Xw}$	Zonal wind component (west-east)
$\vec{Yw}$	Meridional wind component (south-north)
ΔXw	Altitudinal difference in zonal wind speed
ΔYw	Altitudinal difference in meridional wind speed

See Fig. 2 for a representation of the vectors.

Table 2
Summary of the wind conditions and flight characteristics averaged over each section (departure and return) for 79 foraging trips of Antarctic petrels from Svarthammaren breeding colony, Dronning Maud Land, Antarctica

Trip section	Wind conditions (mean±SD)			Bird flight characteristics (mean±SD)						
	Speed Vw (m/s)	Wind support Vs (m/s)	Cross wind |Vc|(m/s)	Airspeed Va (m/s)	Ground velocity Vg (m/s)	Height (m)	Duration (h)	Length (km)	Ground track direction (°)	Heading (°)
Departure	9.1±4.8	−2.5±4.2**	8.1±4.2**	14.5±2.0	15.3±2.3*	893±527*	4.3±0.9	238±44	344±18	016±13
Range	[0; 37.1]	[−28.5; 21.9]	[0; 33.1]	[0.4; 38.2]	[0.1; 39.16]	[0; 3021]	[2.6; 6.6]	[187; 383]	[313; 028]	[346; 049]
Return	8.4±5.4†	−5.6±5.6	5.1±3.0	14.3±3.0†	10.9±3.6	694±424	5.8±2.4**	297±89**	183±21	147±33
Range	[0.1; 33.4]	[−33.1; 16.3]	[0; 24.1]	[0.2; 40.4]	[0.1; 33.8]	[0; 3170]	[3.3; 14.7]	[190; 646]	[099; 220]	[078; 215]

Negative values for wind support (Vs) indicate head winds. For cross winds (Vc) absolute values were used. When relevant, we tested for differences in average parameter values at departure versus return using paired *t* tests. The ground velocity represents the net displacement averaged over each section. Ground track direction and heading values are relative to geographical north. Height values are in metres above ground level. Duration and length were calculated from interpolated locations between the colony and the ice shelf boundary to ensure that these parameters were comparable among tracks.
[†] $P > 0.3$; [*] $P < 0.005$; [**] $P < 0.001$; paired *t* tests.

season. These commuting trips represent on average 21% (range 5−53) of the total distance covered by Antarctic petrels during their complete foraging, i.e. including the section over the ocean (Descamps, 2014). The flight profiles (flight height plotted against time; Fig. 3) ranged between two extremes: birds flying high and showing a bell-shaped profile with gradual ascent and descent or birds continuously flying very close to the ground. The highest flying height observed was 3170 m while the highest absolute altitude was 3478 m asl. In spite of strong interindividual variation, birds seemingly drifted to the west both during departure and return (Fig. 1). There was a tendency (61% of all return sections) to return to the colony either from the north or northeast (Fig. 1b). Associated with westward drift during departure, this generated a clockwise looping pattern in the foraging trips.
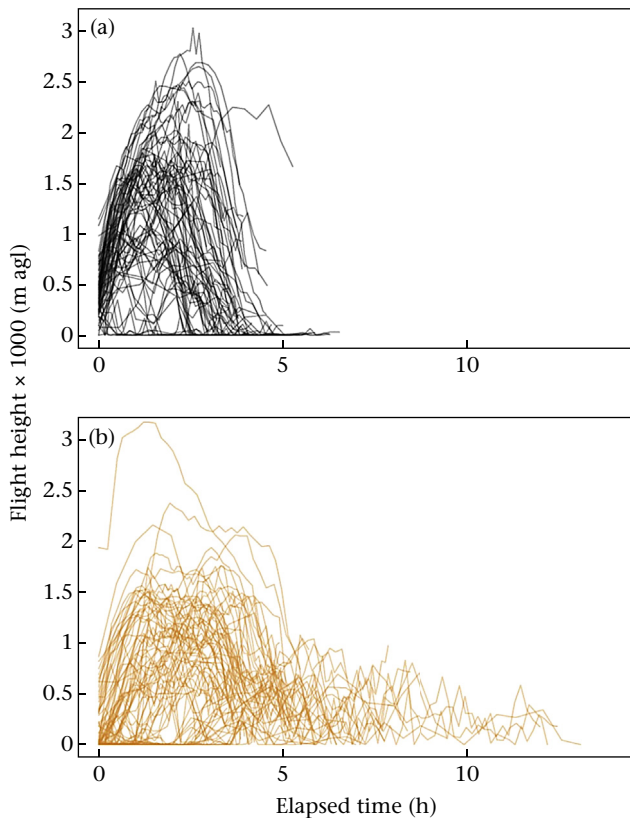

Figure 3. Flight profiles. Flying height (m above ground level) versus time elapsed since the flight started for 79 tracks of Antarctic petrels from the Svarthamaren breeding colony, Dronning Maud Land, Antarctica, during both (a) departure and (b) return flights.

Wind Conditions and Flight Response while Commuting

Commuting Antarctic petrels encountered particularly unfavourable wind conditions. The highest absolute wind speed estimated while flying was 37.1 m/s, which is equivalent to a hurricane on the Beaufort scale. In about one-third of the trips, the average wind speed over a given section (i.e. either departure or return; see Fig. 1), was >11.0 m/s. Birds tended to encounter slightly stronger winds during departing than during returning flights (Table 2). They had to cope with strong zonal (Xw) but weaker meridional (Yw) winds during both departure and return (Fig. 1). Average Xw was nearly always negative during both departure and return flights, indicating rather stable westward prevailing winds (Figs. 1, 4).

Antarctic petrels tended, on average, to fly with some head wind component (Vs < 0) during both sections, but the head wind component was stronger by 3.1 m/s (95% CI = [1.6; 4.6]) during returns (Table 2, Fig. 1). The variation was high, however, as 34% and 12% of the tracks were characterized by average Vs ≥ 0 (favourable wind support component) for departure and return, respectively. During return, average ground velocity was lower, with birds moving on average 29% (4.4 m/s, 95% CI = [3.6; 5.2]) slower in terms of net displacement. Some of the returning birds made it almost directly to the colony, although most of them drifted much farther west before abruptly changing their flight direction and following the nunatak mountain range until they eventually reached the colony (Fig. 1). As a consequence, they flew over distances that were on average 59 km (95% CI = [39; 79]) longer than during departure (Table 2). By doing so, they also flew nearby, and sometimes right above, the neighbouring Jutulsessen breeding colony (Fig. 1; van Franeker et al., 1999; Mehlum et al., 1988). Owing to a lower average ground velocity and longer distance travelled, return trips lasted 37% longer than departure trips (1.6 h, 95% CI = [1.1; 2.1]; Table 2).

Compensation and Drift (Predictions 1 and 2)

Average airspeed was similar in both trip sections (Table 2), but returning birds responded by a sharper increase in average airspeed in the strongest westward winds (Xw < −10 m/s; Fig. 4a). The ground distance covered was also significantly higher in strong westward winds for both departure and return (Fig. 4b), indicating that birds drifted westward with the wind in both cases. Xw influenced ground distance covered during both departure and return (*F* tests: departure: $F_{2, 76} = 34.4$, $P < 0.001$; return: $F_{2, 76} = 5.4$, $P < 0.01$), and accounted for as much as 47.5% of the variance at departure, but only 12.4% at return (Fig. 4b).
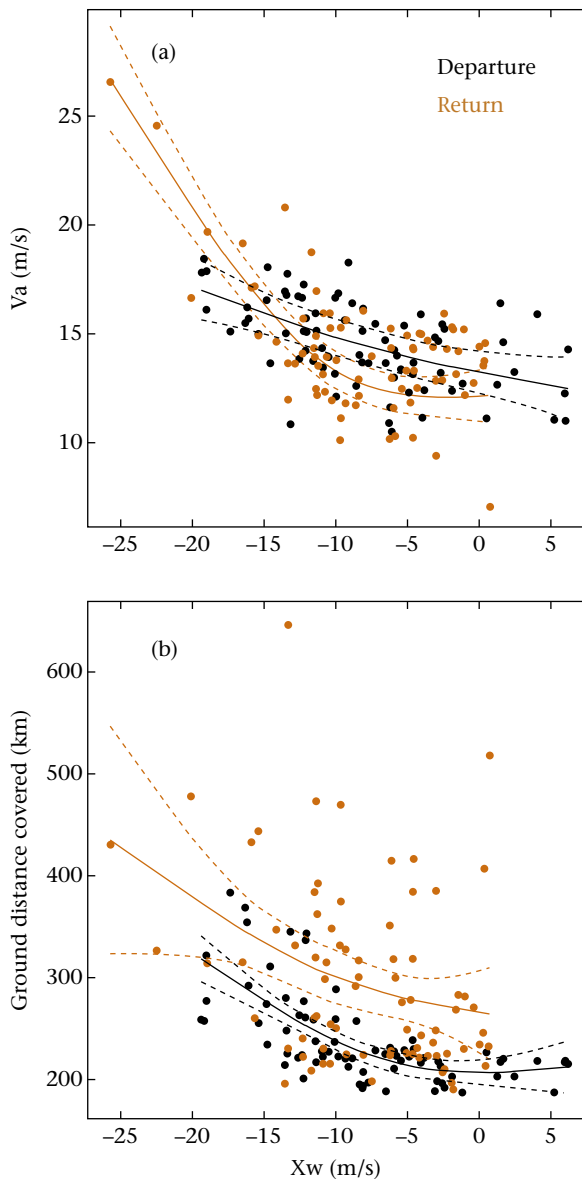
Figure 4. Effect of the zonal wind component (Xw) on (a) the airspeed (Va) and (b) the ground distance covered during departure (black circles and curves) and return (orange circles and curves) commuting flights of Antarctic petrels breeding in Dronning Maud Land, Antarctica. Solid lines show the fitted response curves ($\pm$2SE, dashed lines) from additive models.

Figure 5. Results of a linear regression of the mean ground track direction (γ) on the difference (δ) between the ground track direction ($\overrightarrow{Vg}$) and the bird's heading, or airspeed ($\overrightarrow{Va}$), at departure. Ground track directions are expressed as deviation from geographical north. The preferred flight direction corresponds to the heading of the birds in tail winds or calm winds (Green & Alerstam, 2002).
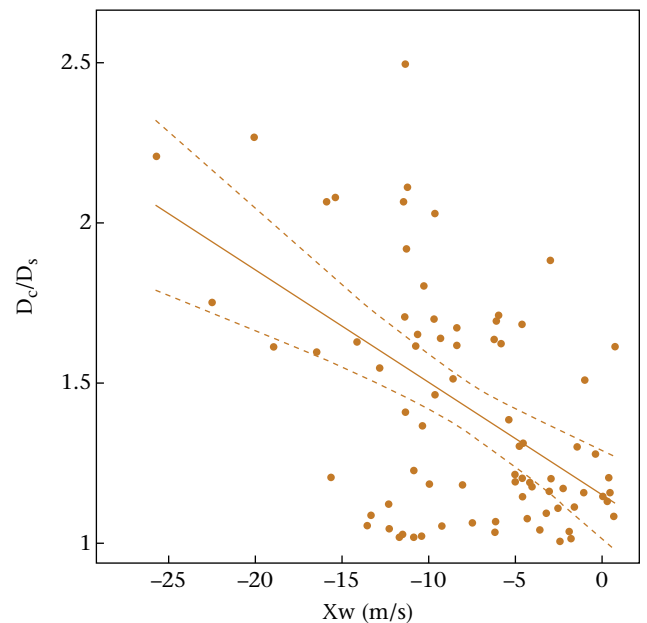
Figure 6. Effect of the zonal wind component (Xw) on the distance ratio during return flights for 79 foraging trips of Antarctic petrels from the Svarthamaren breeding colony, Dronning Maud Land, Antarctica. D_c corresponds to the actual ground distance covered by an individual, while D_s is the straight-line distance between the first location of the return section and the breeding colony. In other words, D_s corresponds to the length of the shortest path a bird could have taken from the location where its return journey started. Details are in Methods: Statistical Analyses.

The regression slope quantifying the average magnitude of drift at departure was $b = 0.66$ (95% CI = [0.56; 0.76]; Fig. 5), showing only limited compensation. The intercept of the regression model indicated a preferred flight direction, i.e. the heading of the birds in tail winds or calm winds (Green & Alerstam, 2002), of 5° (95% CI = [1; 9]; Fig. 5). We could not apply the same approach to return flights (see Statistical Analyses above). However, we found a strong effect of Xw on the straightness of return flights (Fig. 6): in strong westward winds the actual distance covered was at times over twice the straight-line distance, indicating that strong winds altered the return paths. Furthermore, the complementary examination of the wind effect Vg−Va, or 'speed increment due to wind' (Shamoun-Baranes et al., 2007), showed a systematic negative wind effect on birds that were following the mountain range before reaching the colony (Fig. 7).
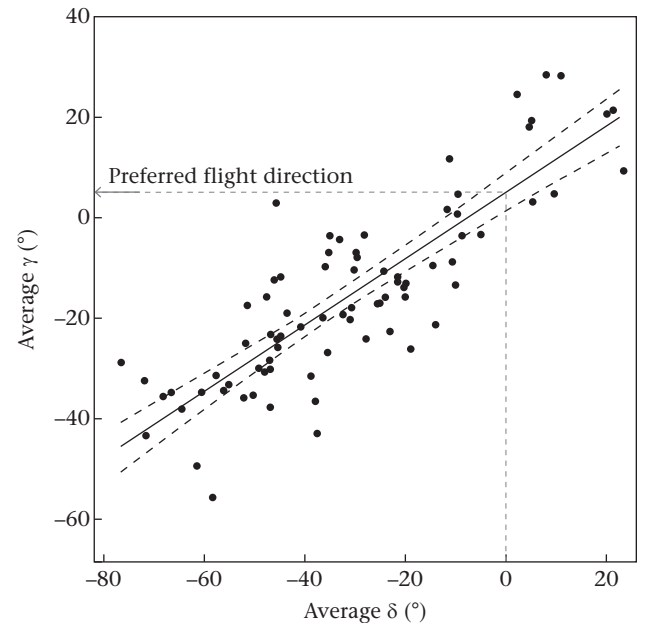
Selection of Flight Height (Prediction 3)

Average flight height was variable but slightly higher during departure than return sections (Table 2). Birds flew closer to ground level in strong westward winds (i.e. more negative values of Xw)
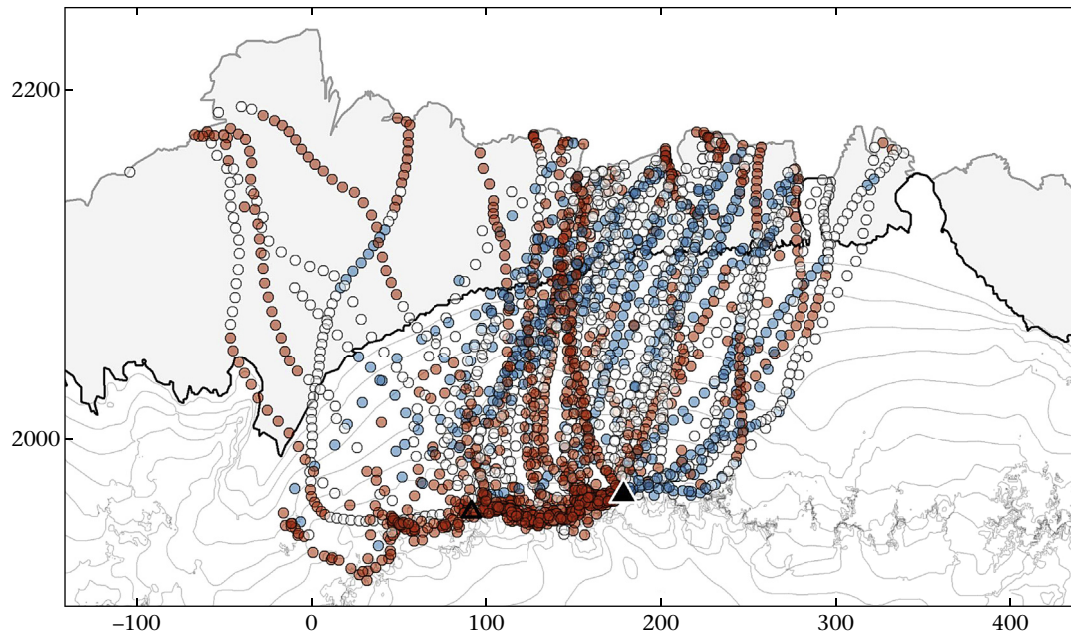
Figure 7. Map of the return sections of 79 foraging trips of Antarctic petrels from the Svarthamaren breeding colony, Dronning Maud Land, Antarctica. The magnitude of the wind effect (Vg−Va; for details see e.g. Shamoun-Baranes et al., 2007) is indicated by the colour, with blue showing more positive values (interval = [2; 16 m/s]) and red more negative values (interval = [−32; −2 m/s]) of the wind effect on the ground speed. Empty circles indicate a negligible wind effect (interval = [−2; 2 m/s]). The locations of the study breeding colony (Svarthamaren; filled triangle) and that of a neighbouring colony (Jutulsessen: empty triangle) are also indicated. The elevation contour lines are separated by 200 m. Map projection is Polar Stereographic. All projected coordinates are in km along the X- and Y-axis. Continent and ice shelf data are from Scambos et al. (2007), and elevation contour lines were derived from the Radarsat Antarctic Mapping Project (RAMP2) Digital Elevation Model (Liu, Jezek, Li, & Zhao, 2001).

during both departure and return (Table 3; Fig. 8a). Departing birds flew higher when a northward wind component was present (positive Yw), but this effect was not statistically significant for returning birds (Table 3; Fig. 8b). Flying height was also modelled as a smoothed function of Vs and the absolute Vc (|Vc|), in order to investigate the effect of the wind relative to the bird's heading, i.e. irrespective of the absolute wind direction. Birds flew lower in head winds than tail winds (Fig. 8c). Birds also tended to fly lower in cross winds, although this effect was only statistically significant during return flights (Table 3; Fig. 8d).

Both departing and returning birds flew at heights with weaker Xw and Yw than what they would have encountered if flying above their actual flight height (all effects were statistically significant; Table 4; Fig. 9a, c), unless wind conditions were calm (i.e. Xw and Yw around 0 m/s). Overall, wind conditions (Xw or Yw) above always explained a much larger proportion (range 30.0–77.4%) of the variance in ΔXw or ΔYw at the bird's flight height, compared to that

explained by the wind conditions below (range 0.8–36.4%; Table 4; Fig. 9b, d). However, conditions below also had a significant effect on both ΔXw and ΔYw for departing birds, with 18.8 and 36.4% of the variance explained, respectively.

DISCUSSION

Our study system offers a unique observational setting due to the combined high altitude, remoteness of the breeding site (absence of food resources in vast surrounding areas) and strong prevailing westward winds. These winds were generally unfavourable to birds flying along a south-north axis. The 6400 km minimum cumulated distance per breeding season that Antarctic petrels fly while commuting over inhospitable areas is larger than that involved in, for example, a typical transatlantic migration flight (Bulte et al., 2014). Given the substantial proportion of the total distance covered in a complete foraging trip that it represents, tactics minimizing time and energy spent during these commuting flights are likely to have evolved. During active flight, birds can adapt to wind conditions through five different orientation responses (sensu Chapman et al., 2011): they can (1) fully drift with the wind; (2) partially compensate; (3) fully compensate; (4) overcompensate (i.e. adjust heading more than necessary); and (5) fly upstream (i.e. against the air flow). In addition, they can select altitudes where wind conditions are more favourable (Dokter, Shamoun-Baranes, Kemp, Tijm, & Holleman, 2013; Mateos-Rodríguez & Liechti, 2011). Our results suggest that Antarctic petrels opt for an intermediate solution between full drift with the wind and full compensation. The latter tactic implies greater airspeeds and thus higher energy expenditure than the former, as long as a bird is flying at greater airspeed than its minimum power speed (Vmp, sensu: Pennycuick, 1978; Pennycuick, 1997). Based on power curve estimation equations from Pennycuick (1998), the predicted V_{mp}

Table 3
Output summary for general additive models predicting the flying height as a function of wind components (Fig. 8)

Trip section	% Variance explained	Explanatory variables	F	P
Departure	39.8	s(Xw)	7.4	0.001
		s(Yw)	5.5	0.006
Return	39.5	s(Xw)	14.9	<0.001
		s(Yw)	0.7	0.510
Departure	33.6	s(Vs)	4.5	0.014
		s(Vc)	1.5	0.230
Return	37.7	s(Vs)	7.2	0.001
		s(Vc)	5.7	0.005

Models were of the form Y ~ s(x₁) + s(x₂), where Y is the average flight height and s(x₁) and s(x₂) were smoothing functions of wind components. All models were constrained to use 2 *df* for each smoothed variable in order to avoid overfitting. $N = 79$ for each model.
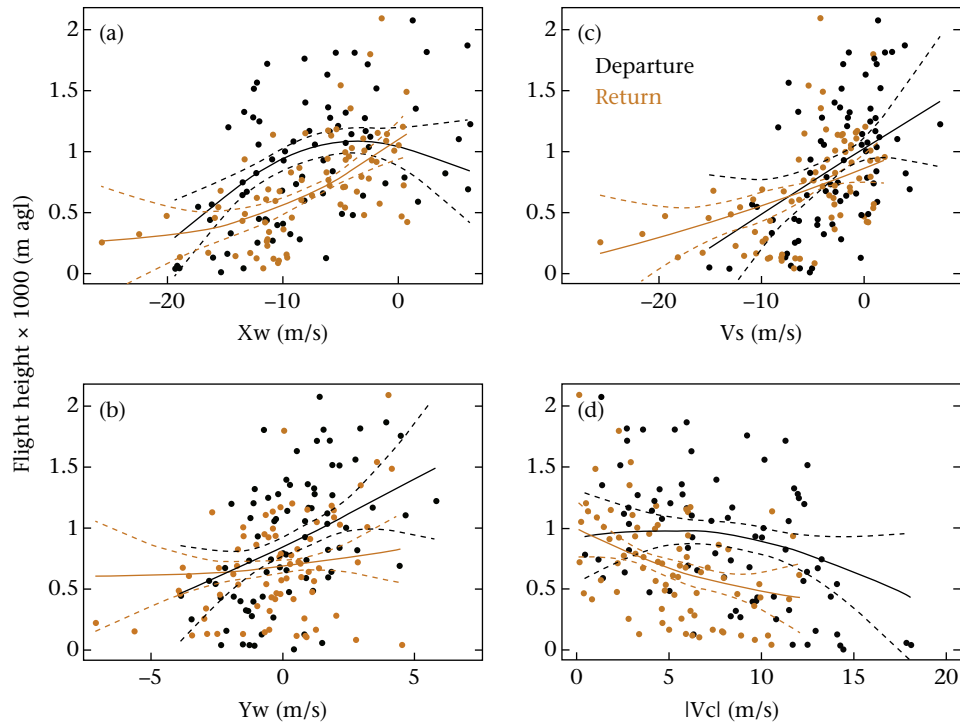
Figure 8. Average flight height (m above ground level) as a function of wind components during departure (black filled circles and curves) and return (orange filled circles and curves). Curves show the partial fitted response from additive models (±2SE, dashed lines). Note that scale varies between panels. (a) Modelled partial effect of the zonal wind (Xw) component. (b) Modelled partial effect of the meridional wind (Yw) component. (c) Modelled partial effect of the wind support (Vs) component. (d) Modelled partial effect of the absolute cross-wind (|Vc|) component.

for an average Antarctic petrel should be approximately 12.0 m/s, and any increase in airspeed past this threshold requires an exponential increase in muscle power and thus in energetic expenditure per unit time (Pennycuick, 1997). Flexible tactics resulted in different responses to the wind conditions during departing versus returning flights. Antarctic petrels only partially adjusted their ground tracks by increasing airspeed in stronger winds while tolerating a certain amount of drift. Returning birds occasionally oriented upstream into strong head winds, with maximum airspeed values reaching >40 m/s. Finally, they generally selected flight heights with more favourable wind conditions.

Wind Conditions and Flight Response while Commuting

A general pattern emerged as tracks followed a clockwise loop with birds drifting westward at departure as well as return, but generally starting the return flight from locations situated further east than their colony. This suggests that at least some of the tracked individuals managed to benefit from the westward winds

at return and used the drift to reach their colony more easily, as some sub-Antarctic seabirds do (Weimerskirch, Guionnet, Martin, Shaffer, & Costa, 2000). Further north, where Antarctic petrels forage (Fauchald & Tveraa, 2003) winds predominantly blow eastwards (westerlies; Parish & Bromwich, 2007), which would be sufficient to generate such a pattern.

Compensation and Drift (Predictions 1 and 2)

Our first prediction was confirmed: departing birds compensated only partially, thus experiencing a westward drift the extent of which varied with wind strength. This behaviour can be expected when the goal is far with respect to the additional ground distance covered due to the drift (Green & Alerstam, 2002; Liechti, 1995) and when it is not a specific location but a large area (Alerstam, 2011). Indeed, the area patrolled by Antarctic petrels from Svarthamaren while foraging at sea can cover hundreds of thousands of km² (Fauchald & Tveraa, 2003). In calm or favourable wind conditions, Antarctic petrels adopted an almost perfect north heading (5°),

Table 4
Output summary for general additive models predicting the difference in wind components (ΔXw or ΔYw) at the birds' locations versus above or below (Fig. 9)

Comparison to wind conditions	Response variable	Trip section	% Variance explained	F	P
Above	ΔXw	Departure	77.4	130.2	<0.001
		Return	52.4	41.8	<0.001
	ΔYw	Departure	62.1	62.3	<0.001
		Return	30.0	16.3	<0.001
Below	ΔXw	Departure	18.8	8.7	<0.001
		Return	0.8	0.3	0.727
	ΔYw	Departure	36.4	21.5	<0.001
		Return	7.4	3.0	0.054

Models were of the form Y ~ s(x), where Y is ΔXw or ΔYw, and s(x) is a smoothing function of the corresponding wind component (Xw or Yw) above or below. All models were constrained to use 2 *df* for the unique smoothed variable in order to avoid overfitting. *N* = 79 for each model.
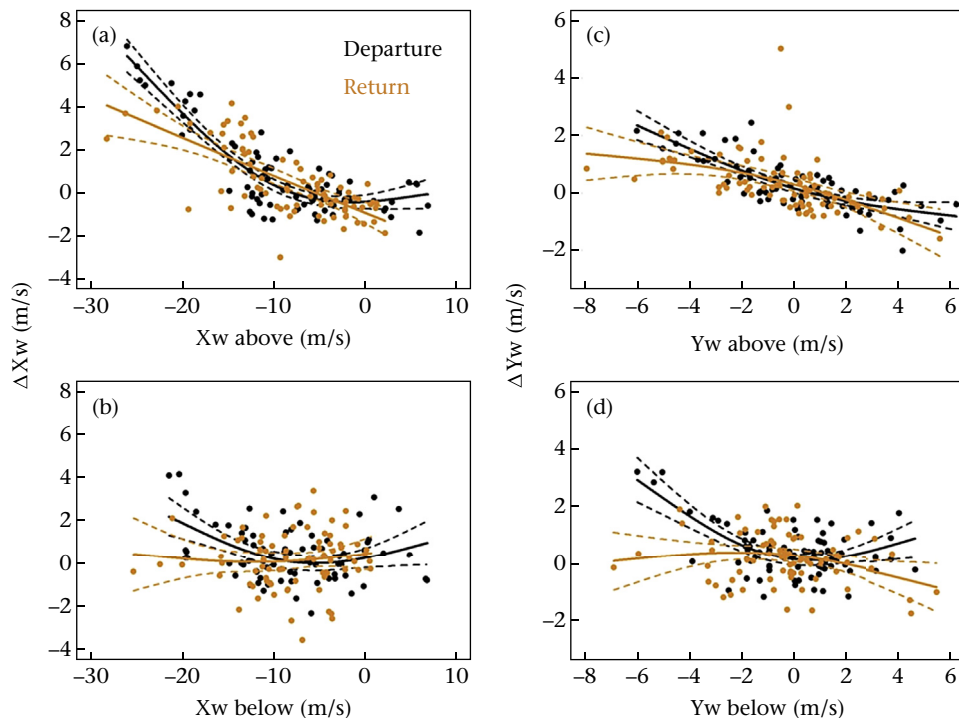
Figure 9. Differences in wind conditions at bird height as a function of the wind conditions at other height levels, both during departure (black filled circles and curves) and return (orange filled circles and curves). Curves show the fitted response (±2SE, dashed lines) from additive models. Note that scale varies between panels. On all panels, values on the Y-axis are negative when the wind component at bird's height is smaller than the wind component below or above bird's height. As a consequence, if the wind component, for example Xw below, is negative (meaning westward wind), then a negative ΔXw would mean that the absolute wind speed at the bird's height is higher than below for that component. Conversely, a positive ΔXw would mean that the absolute wind speed at the bird's height is lower than below for that component. (a) Y-axis: difference in the average zonal wind (Xw) component at bird's height; X-axis: average zonal wind component within the air space up to 400 m above bird's height. (b) Y-axis: difference in the average zonal wind (Xw) component at bird's height; X-axis: average zonal wind component within the air space down to 400 m below bird's height. (c) Y-axis: difference in the average meridional wind (Yw) component at bird's height; X-axis: average meridional wind component within the air space up to 400 m above bird's height. (d) Y-axis: difference in the average meridional wind (Yw) component at bird's height; X-axis: average meridional wind component within the air space down to 400 m below bird's height.

which corresponds well to the direction of the shortest path from their colony to the nearest potential foraging area (i.e. at the boundary of the continental ice shelf; Fig. 1). However, the frequent occurrence of drift shows that the advantage of maintaining this ideal direction diminishes rapidly as wind speed, and the energetic costs associated with compensating for this wind, increases.

Our second prediction (stronger compensation during returning flights) was not supported by our data: at return, the general pattern was the occurrence of a first phase of drift followed by a shorter phase of complete compensation into head winds, which overall led to longer ground distances covered compared to departing flights. This pattern generated curved tracks which fit well the predicted trajectory shapes of birds that are either not compensating or only partially compensating (see figure 2 in Alerstam, 1979b). Assuming that the goal of each individual is to fly directly to its colony, these tracks seemingly correspond to suboptimal trajectories for displacements in flows, as shown theoretically by Hays et al. (2014). The late complete compensation phase, which induced higher airspeed values and consequently higher energy expenditure (Pennycuick, 1997), corresponds to 'upstream orientation' as described by Chapman et al. (2011), and is expected to occur more frequently the closer a travelling animal gets to its goal (Alerstam, 1979b; Chapman et al., 2011; Hays et al., 2014; Liechti, 1995). Several nonmutually exclusive explanations can be proposed.

First, we have shown that most returning individuals fully compensate for wind drift only towards the end of their journey. Inability to properly assess drift could cause such a pattern and has often been suggested as a cause of drift in birds migrating at night

(Alerstam, 1979a; Liechti, 2006; Richardson, 1990) or over sea (Alerstam & Pettersson, 1977), i.e. when landmarks are lacking. Compensation requires the capacity for a bird to precisely assess its current location and that of its destination (Alerstam & Pettersson, 1977; Gould, 1998) as well as the amount of drift to which it is subjected (Alerstam & Gudmundsson, 1999; Liechti, 2006). Our results suggest that this ability may be hindered in Antarctic seabirds flying above the ice cap, potentially due to the absence of noticeable features on the ground, further accentuated by snow drift in strong winds. In contrast, mountain ranges such as those present in our study area create well-delineated and obvious series of landmarks (Fig. 1) that mark the way back to the colony. Antarctic petrels might thus be more limited by their ability to assess drift than by their ability to compensate for it.

Second, Antarctic petrels could potentially use orographic lift (upward air streams generated by mountain slopes; Bohrer et al., 2012) along the nunatak range in order to gain altitude (Duriez et al., 2014), using an energy-efficient flying tactic close to that of geese migrating over the Himalaya (Bishop et al., 2015). In such a case, the overall energetic costs of the longer return flights could be less than that of a more direct flight with strong compensation. Accelerometry (flapping versus soaring flight) and physiological (heart beat) data would help to confirm or refute this hypothesis (Bishop et al., 2015; Duriez et al., 2014). Our results clearly show, however, that birds almost systematically flew against the wind in this portion of the return trip, whether orographic lift occurred or not.

Third, Antarctic petrels are known to fly and forage in large flocks (Ainley, O'Connor, & Boekelheide, 1984), and gregariousness

might thus have affected the trajectories of the tracked individuals. Several individuals flew near the neighbouring Jutulsessen colony, situated ca. 100 km west of the Svarthamaren colony (Fig. 1) and hosting >30 000 breeding pairs (van Franeker et al., 1999). Birds from Svarthamaren may have followed birds breeding at Jutulsessen on their way back. This behaviour could also indicate an attempt to gather so-called public information on nesting site quality or breeding success of conspecifics at another site, as has been observed in other colonial seabirds (Boulinier, McCoy, Yoccoz, Gasparini, & Tveraa, 2008; Grémillet & Boulinier, 2009).

Selection of Flight Height (Prediction 3)

Our third prediction was confirmed, showing that commuting Antarctic petrels selected flight heights at which conditions were usually more favourable, similarly to tactics adopted by migrating birds (Alerstam, 1979b; Mateos-Rodríguez & Liechti, 2011). However, some variation remained unexplained by the wind conditions, particularly below the bird's flying height. In head winds and stronger cross winds birds flew closer to ground level, where wind strength is typically lower than at altitude (Liechti, 2006). In calm conditions or in tail winds they flew relatively high, up to 3170 m. This suggests that, in addition to encountering more favourable wind conditions, there might be other advantages to flying at higher heights for commuting Antarctic petrels. Active flight at high altitudes has been observed in numerous migrating birds (Bishop et al., 2015; Dokter et al., 2013; Mateos-Rodríguez & Liechti, 2011). Advantages of flying higher include optimal use of favourable winds (Alerstam, 1979b; Mateos-Rodríguez & Liechti, 2011), better ability to detect landmarks situated far on the horizon line (e.g. mountains) and reduced transport costs per unit distance covered (Liechti, 2006; Pennycuick, 1975; Schmaljohann & Liechti, 2009). However, flying higher increases the difficulty of estimating drift based on visible ground features (Chapman et al., 2011; Liechti, 2006). Selection of flight height may thus result from a trade-off between lower energy expenditure and better orientation, and varies with the species considered and the environmental conditions (Dokter et al., 2013; Liechti, 2006). One should therefore expect birds to fly at lower altitudes when the need to assess the drift is higher, which corresponds to what was observed. Antarctic petrels flew lower only in strong winds, i.e. when the risk of excessive drift was highest. However, when possible, flying higher should allow better and earlier detection of remote landscape features such as polynyas and leads in sea ice on the way to foraging areas, or mountain ranges and potential colonies during return flights.

Conclusion

Antarctic petrels used flexible tactics in response to wind conditions, flying lower and drifting more in the strongest wind, or flying higher in more favourable winds. Distinguishing between real adaptations to perceived conditions and suboptimal behavioural responses due to the individual's inability to assess these conditions has been identified as a major challenge (Chapman et al., 2011). Our results suggest that Antarctic petrels might be more limited by their ability to precisely assess drift than by their ability to compensate for it. Furthermore, it has been shown that colonies located downwind of foraging areas theoretically provide the ideal solution for seabirds that, when returning to their nest with higher food loads, can then take advantage of favourable tail winds (Pennycuick, 1989; Spear & Ainley, 1997a). According to these studies, and from a flight costs' perspective, the colony location in our study system appears to be suboptimal and, due to similar wind patterns in other parts of Antarctica (Parish & Bromwich, 2007;

Turner et al., 2005), one might expect that most other flying seabird colonies situated inland in Antarctica are in a similar situation. This indicates the likely occurrence of compensating benefits for individuals nesting in those colonies. Expected changes in wind patterns in Antarctica (Turner et al., 2005) could affect flying seabirds by increasing drift levels during commuting flights, and thus put additional energy constraints by increasing the cost of active flight, in particular during inbound flights. While adults might be able to cope with additional energy expenditure due to unfavourable wind conditions without any effect on their own survival, an increase in travel time or a deterioration of their body condition would probably have detrimental effects on their reproductive success (Tveraa, Sether, Aanes, & Erikstad, 1998).

References

Agostinelli, C., & Lund, U. (2013). *R package 'circular': Circular statistics* Accessed at: https://r-forge.r-project.org/projects/circular.

Ainley, D. G., O'Connor, E. F., & Boekelheide, R. J. (1984). The marine ecology of birds in the Ross Sea, Antarctica. *Ornithological Monographs, 32*, 1–97.

Alerstam, T. (1979a). Optimal use of wind by migrating birds: combined drift and overcompensation. *Journal of Theoretical Biology, 79*, 341–353.

Alerstam, T. (1979b). Wind as selective agent in bird migration. *Ornis Scandinavica, 10*, 76–93.

Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology, 152*, 5–23.

Alerstam, T., & Gudmundsson, G. A. (1999). Bird orientation at high latitudes: flight routes between Siberia and North America across the Arctic Ocean. *Proceedings of the Royal Society B: Biological Sciences, 266*, 2499–2505.

Alerstam, T., & Pettersson, S.-G. (1977). Why do migrating birds fly along coastlines? *Journal of Theoretical Biology, 65*, 699–712.

Amélineau, F., Péron, C., Lescroël, A., Authier, M., Provost, P., & Grémillet, D. (2014). Windscape and tortuosity shape the flight costs of northern gannets. *Journal of Experimental Biology, 217*, 876–885.

Bale, R., Hao, M., Bhalla, A. P. S., & Patankar, N. A. (2014). Energy efficiency and allometry of movement of swimming and flying animals. *Proceedings of the National Academy of Sciences of the United States of America, 111*, 7517–7521.

Batschelet, E. (1981). *Circular statistics in biology*. London, U.K.: Academic Press.

Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., et al. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science, 347*, 250–254.

Bohrer, G., Brandes, D., Mandel, J. T., Bildstein, K. L., Miller, T. A., Lanzone, M., et al. (2012). Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecology Letters, 15*, 96–103.

Boulinier, T., McCoy, K. D., Yoccoz, N. G., Gasparini, J., & Tveraa, T. (2008). Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters, 4*, 538–540.

Bromwich, D. H., Otieno, F. O., Hines, K. M., Manning, K. W., & Shilo, E. (2013). Comprehensive evaluation of polar weather research and forecasting model performance in the Antarctic. *Journal of Geophysical Research: Atmospheres, 118*, 274–292.

Bulte, M., McLaren, J. D., Bairlein, F., Bouten, W., Schmaljohann, H., & Shamoun-Baranes, J. (2014). Can wheatears weather the Atlantic? Modeling nonstop trans-Atlantic flights of a small migratory songbird. *Auk, 131*, 363–370.

Calenge, C. (2006). The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling, 197*, 516–519.

Chapman, J. W., Klaassen, R. H. G., Drake, V. A., Fossette, S., Hays, G. C., Metcalfe, J. D., et al. (2011). Animal orientation strategies for movement in flows. *Current Biology, 21*, R861–R870.

Descamps, S. (2014). *[GPS tracking data of Antarctic petrels* Thalassoica antarctica *from Svarthamaren breeding colony, Dronning Maud Land]* (Unpublished raw data).

Descamps, S., Tarroux, A., Lorentsen, S.-H., Love, O. P., Varpe, Ø., & Yoccoz, N. G. (2015). Large-scale oceanographic fluctuations drive Antarctic petrel survival and reproduction. *Ecography*. http://dx.doi.org/10.1111/ecog.01659.

Descamps, S., Tarroux, A., Varpe, Ø., Yoccoz, N. G., Tveraa, T., & Lorentsen, S.-H. (2015). Demographic effects of extreme weather events: snow storms, breeding success, and population growth rate in a long-lived Antarctic seabird. *Ecology and Evolution, 5*, 314–325.

Dokter, A. M., Shamoun-Baranes, J., Kemp, M. U., Tijm, S., & Holleman, I. (2013). High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. *PLoS One, 8*, e52300.

Duriez, O., Kato, A., Tromp, C., Dell'Omo, G., Vyssotski, A. L., Sarrazin, F., et al. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLoS One, 9*, e84887.

Elliott, K., Chivers, L., Bessey, L., Gaston, A., Hatch, S., Kato, A., et al. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology, 2*, 17.

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proceedings of the National Academy of Sciences of the United States of America, 110*, 9380–9384.

Fauchald, P., & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology, 84*, 282–288.

Fauchald, P., & Tveraa, T. (2006). Hierarchical patch dynamics and animal movement pattern. *Oecologia, V149*, 383–395.

van Franeker, J. A., Gavrilo, M., Mehlum, F., Veit, R. R., & Woehler, E. J. (1999). Distribution and abundance of the Antarctic petrel. *Waterbirds, 22*, 14–28.

Fritz, H., Said, S., & Weimerskirch, H. (2003). Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society B: Biological Sciences, 270*, 1143–1148.

Gould, J. L. (1998). Sensory bases of navigation. *Current Biology, 8*, R731–R738.

Green, M., & Alerstam, T. (2002). The problem of estimating wind drift in migrating birds. *Journal of Theoretical Biology, 218*, 485–496.

Grémillet, D., & Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series, 391*, 121–137.

Hays, G. C., Christensen, A., Fossette, S., Schofield, G., Talbot, J., & Mariani, P. (2014). Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. *Ecology Letters, 17*, 137–143.

Houston, A. I. (2006). The flight speed of parent birds feeding young. *Journal of Avian Biology, 37*, 545–554.

Karlsson, H., Henningsson, P., Bäckman, J., Hedenström, A., & Alerstam, T. (2010). Compensation for wind drift by migrating swifts. *Animal Behaviour, 80*, 399–404.

Kemp, M. U., Shamoun-Baranes, J., Van Gasteren, H., Bouten, W., & Van Loon, E. E. (2010). Can wind help explain seasonal differences in avian migration speed? *Journal of Avian Biology, 41*, 672–677.

Klaassen, R. H. G., Hake, M., Strandberg, R., & Alerstam, T. (2010). Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proceedings of the Royal Society B: Biological Sciences, 278*, 1339–1346.

La, H. S., Lee, H., Fielding, S., Kang, D., Ha, H. K., Atkinson, A., et al. (2015). High density of ice krill (*Euphausia crystallorophias*) in the Amundsen sea coastal polynya, Antarctica. *Deep Sea Research Part I: Oceanographic Research Papers, 95*, 75–84.

Liechti, F. (1995). Modelling optimal heading and airspeed of migrating birds in relation to energy expenditure and wind influence. *Journal of Avian Biology, 26*, 330–336.

Liechti, F. (2006). Birds: blowin' by the wind? *Journal of Ornithology, 147*, 202–211.

Liu, H., Jezek, K. C., & Li, B. (1999). Development of an Antarctic digital elevation model by integrating cartographic and remotely sensed data: a geographic information system based approach. *Journal of Geophysical Research: Solid Earth, 104*, 23199–23213.

Liu, H., Jezek, K., Li, B., & Zhao, Z. (2001). *Radarsat Antarctic mapping project digital elevation model version 2* Accessed at: http://nsidc.org/data/nsidc-0082.html.

Lorentsen, S.-H., & Røv, N. (1995). Incubation and brooding performance of the Antarctic petrel *Thalassoica antarctica* at Svarthamaren, Dronning Maud Land. *Ibis, 137*, 345–351.

Louzao, M., Wiegand, T., Bartumeus, F., & Weimerskirch, H. (2014). Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: an example with wandering albatrosses. *Movement Ecology, 2*, 8.

Maina, J. N. (2000). What it takes to fly: the structural and functional respiratory refinements in birds and bats. *Journal of Experimental Biology, 203*, 3045–3064.

Mateos-Rodríguez, M., & Liechti, F. (2011). How do diurnal long-distance migrants select flight altitude in relation to wind? *Behavioral Ecology, 23*, 403–409.

McLaren, J. D., Shamoun-Baranes, J., Dokter, A. M., Klaassen, R. H. G., & Bouten, W. (2014). Optimal orientation in flows: providing a benchmark for animal movement strategies. *Journal of the Royal Society Interface, 11*, 20140588.

Mehlum, F., Gjessing, Y., Haftorn, S., & Bech, C. (1988). Census of breeding Antarctic petrels *Thalassoica antarctica* and physical features of the breeding colony at Svarthamaren, Dronning Maud Land, with notes on breeding Snow petrels *Pagodroma nivea* and South Polar skuas *Catharacta maccormicki*. *Polar Research, 6*, 1–9.

Nihashi, S., & Ohshima, K. I. (2015). Circumpolar mapping of Antarctic coastal polynyas and landfast sea ice: relationship and variability. *Journal of Climate, 28*, 3650–3670.

Niizuma, Y., Takahashi, A., Sasaki, N., Hayama, S.-I., Tokita, N., & Watanuki, Y. (2001). Benefits of mass reduction for commuting flight with heavy food load in Leach's storm-petrel, *Oceanodroma leucorhoa*. *Ecological Research, 16*, 197–203.

Norberg, R. A. (1981). Optimal flight speed in birds when feeding young. *Journal of Animal Ecology, 50*, 473–477.

Norberg, U. M. (1995). How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology, 9*, 48–54.

Parish, T. R., & Bromwich, D. H. (2007). Reexamination of the near-surface airflow over the Antarctic continent and implications on atmospheric circulations at high southern latitudes. *Monthly Weather Review, 135*, 1961–1973.

Pennycuick, C. (1975). Chapter 1: mechanics of flight. In D. Farner, & J. King (Eds.), *Avian biology* (Vol. 5, pp. 1–75). New York, NY: Academic Press.

Pennycuick, C. J. (1978). Fifteen testable predictions about bird flight. *Oikos, 30*, 165–176.

Pennycuick, C. (1989). *Bird flight performance: A practical calculation manual*. Oxford, U.K.: Oxford University Press.

Pennycuick, C. (1997). Actual and 'optimum' flight speeds: field data reassessed. *Journal of Experimental Biology, 200*, 2355–2361.

Pennycuick, C. J. (1998). Computer simulation of fat and muscle burn in long-distance bird migration. *Journal of Theoretical Biology, 191*, 47–61.

Portugal, S. J., Hubel, T. Y., Fritz, J., Heese, S., Trobe, D., Voelkl, B., et al. (2014). Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature, 505*, 399–402.

Powers, J. G., Manning, K. W., Bromwich, D. H., Cassano, J. J., & Cayette, A. M. (2012). A decade of Antarctic science support through AMPS. *Bulletin of the American Meteorological Society, 93*, 1699–1712.

Powers, J. G., Monaghan, A. J., Cayette, A. M., Bromwich, D. H., Kuo, Y.-H., & Manning, K. W. (2003). Real-time mesoscale modeling over Antarctica: the Antarctic Mesoscale prediction system. *Bulletin of the American Meteorological Society, 84*, 1533–1545.

R Development Core Team. (2015). *R: A language and environment for statistical computing* Accessed at: http://www.r-project.org.

Raymond, B., Shaffer, S. A., Sokolov, S., Woehler, E. J., Costa, D. P., Einoder, L., et al. (2010). Shearwater foraging in the southern ocean: the roles of prey availability and winds. *PLoS One, 5*, e10960.

Richardson, W. J. (1990). Wind and orientation of migrating birds: a review. *Experientia, 46*, 416–425.

Scambos, T. A., Haran, T. M., Fahnestock, M. A., Painter, T. H., & Bohlander, J. (2007). MODIS-based Mosaic of Antarctica (MOA) data sets: continent-wide surface morphology and snow grain size. *Remote Sensing of Environment, 111*, 242–257.

Schmaljohann, H., & Liechti, F. (2009). Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds. *Journal of Experimental Biology, 212*, 3633–3642.

Shamoun-Baranes, J., van Loon, E., Liechti, F., & Bouten, W. (2007). Analyzing the effect of wind on flight: pitfalls and solutions. *Journal of Experimental Biology, 210*, 82–90.

Spear, L. B., & Ainley, D. G. (1997a). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis, 139*, 221–233.

Spear, L. B., & Ainley, D. G. (1997b). Flight speed of seabirds in relation to wind speed and direction. *Ibis, 139*, 234–251.

Stirling, I. (1997). The importance of polynyas, ice edges, and leads to marine mammals and birds. *Journal of Marine Systems, 10*, 9–21.

Tarroux, A., Weimerskirch, H., Wang, S.-H., Bromwich, D. H., Cherel, Y., Kato, A., et al. (2015). *Data from: Flexible flight response to challenging wind conditions in a commuting Antarctic seabird: Do you catch the drift? Movebank Data Repository. Movebank ID: 121041109*. http://dx.doi.org/10.5441/001/1.q206rm6b Accessed at: www.movebank.org.

Tucker, V. A., & Schmidt-Koenig, K. (1971). Flight speeds of birds in relation to energetics and wind directions. *Auk, 88*, 97–107.

Turner, J., Chenoli, S. N., abu Samah, A., Marshall, G., Phillips, T., & Orr, A. (2009). Strong wind events in the Antarctic. *Journal of Geophysical Research: Atmospheres, 114*, D18103.

Turner, J., Colwell, S. R., Marshall, G. J., Lachlan-Cope, T. A., Carleton, A. M., Jones, P. D., et al. (2005). Antarctic climate change during the last 50 years. *International Journal of Climatology, 25*, 279–294.

Tveraa, T., Lorentsen, S.-H., & Sæther, B.-E. (1997). Regulation of foraging trips and costs of incubation shifts in the Antarctic petrel (*Thalassoica antarctica*). *Behavioral Ecology, 8*, 465–469.

Tveraa, T., Sether, B.-E., Aanes, R., & Erikstad, K. E. (1998). Regulation of food provisioning in the Antarctic petrel: the importance of parental body condition and chick body mass. *Journal of Animal Ecology, 67*, 699–704.

Urbanek, S. (2012). *proj4: A simple interface to the PROJ.4 cartographic projections library* Accessed at: http://CRAN.R-project.org/package=proj4.

Vansteelant, W. M. G., Bouten, W., Klaassen, R. H. G., Koks, B. J., Schlaich, A. E., van Diermen, J., et al. (2015). Regional and seasonal flight speeds of soaring

migrants and the role of weather conditions at hourly and daily scales. *Journal of Avian Biology, 46*, 25–39.

Varpe, Ø., Tveraa, T., & Folstad, I. (2004). State-dependent parental care in the Antarctic petrel: responses to manipulated chick age during early chick rearing. *Oikos, 106*, 479–488.

Weimerskirch, H., Chastel, O., Barbraud, C., & Tostain, O. (2003). Flight performance: frigatebirds ride high on thermals. *Nature, 421*, 333–334.

Weimerskirch, H., Cherel, Y., Delord, K., Jaeger, A., Patrick, S. C., & Riotte-Lambert, L. (2014). Lifetime foraging patterns of the wandering albatross: life on the move! *Journal of Experimental Marine Biology and Ecology, 450*, 68–78.

Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A., & Costa, D. P. (2000). Fast and fuel efficient? Optimal use of wind by flying Albatrosses. *Proceedings of the Royal Society B: Biological Sciences, 267*, 1869–1874.

Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P., & Jiraskova, S. (2001). Energy saving in flight formation. *Nature, 413*, 697–698.

Wood, S. N. (2006). *Generalized additive models: An introduction with R.* Boca Raton, FL: CRC Press/Taylor & Francis Group.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology), 73*, 3–36.

Zuur, A. F., Saveliev, A. A., & Ieno, E. N. (2014). *A beginner's guide to generalised additive mixed models with R.* Newburgh, U.K.: Highland Statistics Ltd.

APPENDIX

Table A1

Summary parameters calculated for each section (departure and return) of 79 foraging trips of Antarctic petrels from Svarthammaren breeding colony, Dronning Maud Land, Antarctica

Season	Bird ID	Departure section					Return section				
		Departure date	No. of locations	Duration (h)	Total length (km)	Mean track direction γ (° from N)	Return date	No. of locations	Duration (h)	Total length (km)	Mean track direction γ (° from N)
1112	4155777	12 Dec 2011	10	5.7	227	28	29 Dec 2011	14	6.5	347	159
1112	4182444	13 Dec 2011	10	5.4	222	347	31 Dec 2011	7	5.8	260	180
1112	4182101	14 Dec 2011	3	5.0	255	326	05 Jan 2012	2	3.6	210	209
1112	4182103	14 Dec 2011	6	6.5	345	313	29 Dec 2011	8	8.7	314	152
1112	4182111	28 Dec 2011	8	4.5	280	328	10 Jan 2012	8	4.0	232	210
1112	4182133	07 Jan 2012	17	5.5	228	359	15 Jan 2012	19	6.4	348	168
1112	4182135	08 Jan 2012	24	4.0	195	351	17 Jan 2012	30	5.2	281	167
1112	4182008	25 Jan 2012	21	3.5	217	341	01 Feb 2012	23	3.9	216	208
1112	4182006	26 Jan 2012	27	4.8	343	317	31 Jan 2012	22	3.7	223	172
1112	4182006	07 Feb 2012	27	4.5	237	337	14 Feb 2012	23	3.9	215	211
1213	4181880	26 Dec 2012	27	4.4	261	333	09 Jan 2013	30	4.3	268	220
1213	4182155	17 Jan 2013	25	4.2	259	338	23 Jan 2013	31	5.1	278	189
1213	4182157	17 Jan 2013	21	3.4	221	344	23 Jan 2013	27	4.7	226	177
1213	4181979	18 Jan 2013	31	5.2	257	331	24 Jan 2013	29	3.9	198	190
1213	4182154	19 Jan 2013	29	4.8	259	336	25 Jan 2013	25	4.2	230	206
1213	4181998	21 Jan 2013	44	3.7	217	348	26 Jan 2013	67	5.4	276	179
1213	4181999	21 Jan 2013	48	4.0	221	340	28 Jan 2013	57	4.8	248	164
1213	4181993	22 Jan 2013	48	4.1	211	349	28 Jan 2013	40	3.3	222	198
1213	4181994	22 Jan 2013	46	3.8	212	350	27 Jan 2013	50	3.9	236	200
1213	4181995	22 Jan 2013	51	4.5	218	347	29 Jan 2013	60	5.0	315	177
1213	4219220	22 Jan 2013	46	3.8	188	357	25 Jan 2013	40	3.3	196	176
1213	4181903	23 Jan 2013	42	3.5	228	345	29 Jan 2013	62	5.2	254	174
1213	4181984	23 Jan 2013	46	3.8	225	347	27 Jan 2013	41	3.5	228	208
1213	4181991	23 Jan 2013	55	4.6	231	337	29 Jan 2013	94	7.7	415	142
1213	4181996	23 Jan 2013	47	4.0	227	339	27 Jan 2013	45	3.9	243	211
1213	4181929	25 Jan 2013	45	3.7	201	3	28 Jan 2013	44	3.7	260	217
1213	4181984	28 Jan 2013	43	3.7	207	353	02 Feb 2013	54	4.4	246	214
1213	4165821	29 Jan 2013	35	3.0	222	346	04 Feb 2013	49	4.0	250	193
1213	4156903	30 Jan 2013	44	3.6	220	16	03 Feb 2013	40	3.4	225	184
1213	4165818	30 Jan 2013	32	2.6	215	23	05 Feb 2013	45	4.0	225	191
1213	4181987	30 Jan 2013	41	3.4	217	18	04 Feb 2013	47	4.0	230	187
1213	4181988	30 Jan 2013	39	3.0	218	25	05 Feb 2013	36	3.4	209	208
1213	4165837	08 Feb 2013	37	3.3	258	330	12 Feb 2013	50	4.1	207	187
1213	4165845	11 Feb 2013	39	3.3	197	357	15 Feb 2013	62	5.2	327	181
1213	4165847	11 Feb 2013	33	2.8	191	354	16 Feb 2013	44	3.6	225	188
1213	4181967	11 Feb 2013	43	3.6	222	349	15 Feb 2013	65	5.0	291	186
1314	4165855	29 Nov 2013	8	4.0	188	5	05 Dec 2013	8	4.4	213	190
1314	4165857	29 Nov 2013	7	3.9	187	356	19 Dec 2013	23	14.7	430	138
1314	4165864	30 Nov 2013	10	5.7	277	331	18 Dec 2013	13	7.5	443	120
1314	4182164	30 Nov 2013	12	6.6	337	327	21 Dec 2013	18	10.0	433	138
1314	4165868	01 Dec 2013	8	4.4	321	315	15 Dec 2013	11	6.3	332	131
1314	4165871	02 Dec 2013	9	4.7	274	334	18 Dec 2013	13	8.3	478	118
1314	4165872	02 Dec 2013	8	4.1	248	333	20 Dec 2013	12	7.5	315	148
1314	4165854	03 Dec 2013	9	4.4	227	348	15 Dec 2013	19	10.5	473	100
1314	4165874	03 Dec 2013	7	4.2	221	344	15 Dec 2013	15	8.2	392	110
1314	4165875	03 Dec 2013	7	4.8	227	341	11 Dec 2013	11	6.4	331	173
1314	4181878	03 Dec 2013	7	4.3	221	347	31 Dec 2013	14	6.7	320	166
1314	4182043	03 Dec 2013	10	5.3	220	350	14 Dec 2013	13	6.8	298	155
1314	4120679	04 Dec 2013	7	3.7	218	18	11 Dec 2013	7	4.5	240	199
1314	4165870	04 Dec 2013	7	3.1	187	8	20 Dec 2013	13	7.2	326	149
1314	4165855	07 Dec 2013	8	4.6	238	338	16 Dec 2013	13	7.2	384	112
1314	4165881	13 Dec 2013	29	4.8	224	342	28 Dec 2013	46	7.6	385	153
1314	4165894	17 Dec 2013	38	6.3	311	330	27 Dec 2013	34	5.8	318	159
1314	4165895	18 Dec 2013	31	5.9	277	335	29 Dec 2013	36	6.0	301	159
1314	4165896	18 Dec 2013	29	4.7	259	330	01 Jan 2014	30	5.3	262	167

Table A1 (*continued*)

Season	Bird ID	Departure section					Return section				
		Departure date	No. of locations	Duration (h)	Total length (km)	Mean track direction γ (° from N)	Return date	No. of locations	Duration (h)	Total length (km)	Mean track direction γ (° from N)
1314	4165963	26 Dec 2013	28	4.6	288	333	06 Jan 2014	74	12.4	646	121
1314	4165964	28 Dec 2013	21	3.5	214	346	12 Jan 2014	35	5.9	317	170
1314	4165965	29 Dec 2013	22	3.7	193	354	10 Jan 2014	50	8.5	384	132
1314	4165967	30 Dec 2013	24	4.0	234	340	09 Jan 2014	38	6.4	351	181
1314	4155724	31 Dec 2013	22	3.6	225	354	13 Jan 2014	46	7.6	374	159
1314	4165978	04 Jan 2014	21	3.6	212	355	12 Jan 2014	51	8.5	362	145
1314	4165984	06 Jan 2014	36	6.5	383	322	14 Jan 2014	73	12.6	469	122
1314	4165985	06 Jan 2014	31	4.4	292	334	15 Jan 2014	51	8.6	416	132
1314	4181902	06 Jan 2014	37	5.9	369	331	16 Jan 2014	24	4.1	230	186
1314	4165996	07 Jan 2014	40	6.6	354	332	15 Jan 2014	31	5.0	300	162
1314	4165911	08 Jan 2014	27	4.6	237	342	17 Jan 2014	74	13.6	518	125
1314	4181996	10 Jan 2014	25	4.1	263	335	19 Jan 2014	24	3.9	231	213
1314	4165918	11 Jan 2014	22	3.7	224	356	15 Jan 2014	22	3.7	223	195
1314	4155561	15 Jan 2014	21	3.8	216	357	20 Jan 2014	26	4.3	223	193
1314	4165934	15 Jan 2014	28	5.0	230	349	20 Jan 2014	26	4.4	224	177
1314	4165935	15 Jan 2014	24	4.1	229	349	20 Jan 2014	32	5.6	249	171
1314	4165937	16 Jan 2014	21	3.4	203	5	22 Jan 2014	21	3.5	190	190
1314	4182357	18 Jan 2014	21	3.7	217	23	20 Jan 2014	28	4.7	221	173
1314	4182358	18 Jan 2014	24	3.9	203	6	21 Jan 2014	35	5.9	283	157
1314	4182365	20 Jan 2014	20	3.3	198	5	23 Jan 2014	35	5.8	271	205
1314	4182371	20 Jan 2014	18	3.1	192	357	23 Jan 2014	22	3.6	196	181
1314	4182372	20 Jan 2014	19	3.2	196	358	24 Jan 2014	26	4.3	234	167
1314	4182375	21 Jan 2014	23	3.8	203	9	27 Jan 2014	29	7.9	407	124
1314	4182377	21 Jan 2014	26	4.4	223	351	26 Jan 2014	33	5.6	318	170

1112, 1213, and 1314 stand for breeding season 2011–2012, 2012–2013, and 2013–2014, respectively. N refers to the geographical north.

Figure A1. Photograph of a GPS unit positioned on the central tail feathers of an Antarctic petrel from the Svarthamaren breeding colony, Dronning Maud Land, Antarctica (see Methods). Photo: Sébastien Descamps/NPI.

Figure A2. Antarctic petrel outfitted with a tail-mounted GPS unit landing at its nest at the Svarthamaren breeding colony, Dronning Maud Land, Antarctica (see Methods). This picture shows clearly that the GPS unit allows a perfectly normal deployment of the tail feathers in critical aerial manoeuvres such as landing. Photo: Sébastien Descamps/NPI.