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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.

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