

1 **Interactive effects of body mass changes and species-specific morphology on flight behaviour of**
2 **chick-rearing Antarctic fulmarine petrels under diurnal wind patterns**

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4 Running head: Use of winds by Antarctica fulmarine petrels

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14

15 **Abstract**

16 For procellariiform seabirds, wind and body morphology are crucial determinants of flight costs and
17 flight speeds. During chick-rearing, parental seabirds commute frequently to provision their chicks,
18 and their body mass changes between outbound and return legs.

19 In Antarctica, the typical diurnal katabatic winds which blow stronger in the mornings, form a
20 natural experiment to investigate flight behaviours in response to wind conditions.

21 We GPS-tracked three closely related species of sympatrically breeding Antarctic fulmarine petrels
22 which differ in wing loading and aspect ratio and investigated their flight behaviour in response to
23 wind and changes in body mass.

24 All three species reached higher flight speeds under stronger tailwinds, especially on return legs
25 from foraging, when wing loading was increased since birds carried food for their chicks. Flight
26 speeds decreased under stronger headwinds. Antarctic petrels (*Thalassoica antarctica*; intermediate
27 body mass, highest wing loading and aspect ratio) responded stronger to changes in wind speed and
28 direction than cape petrels (*Daption capense*; lowest body mass, wing loading and aspect ratio) or
29 southern fulmars (*Fulmarus glacialis*; highest body mass, intermediate wing loading and aspect
30 ratio). Birds did not adjust their flight direction in relation to wind direction nor maximum distance
31 to nest when they encountered strong headwinds on their outbound commutes. However, birds
32 appeared to adjust the timing of commutes to those hours of the day when headwinds were
33 weakest and they were more likely to encounter favourable tail- and crosswinds.

34 Despite these adaptations to the predictable diurnal wind conditions, birds frequently encountered
35 unfavourably strong headwinds, possibly as a result of weather systems disrupting the katabatics
36 coupled with the need to feed. How the predicted decrease in Antarctic near-coastal wind speeds
37 over the remainder of the century will affect flight costs and breeding success which ultimately
38 drives population trajectories remains to be seen.

39

40 **Keywords:** movement ecology; foraging; optimization; procellariiform; gust-soaring; flight cost;
41 katabatic wind; climate change

42 Introduction

43 Wind is a key feature of the environment that affects the flight costs of birds moving across their
44 landscape to access their foraging grounds and breeding sites (e.g. Safi *et al.* 2013; Shepard *et al.*
45 2013). Flight styles, wing proportions as well as wing loading, which takes body mass and wing shape
46 into account, are key characteristics that determine flight costs under different wind speeds and
47 wind directions (Pennycuick 2008). Procellariiform seabirds are particularly well-adapted to utilise
48 winds for energy-efficient gust-soaring (Pennycuick 1982; Spear & Ainley 1997a; 1997b). This is
49 reflected by their global distribution and biodiversity patterns which peak in the windiest parts of the
50 Southern Ocean (Suryan *et al.* 2008; Davies *et al.* 2010).

51 Depending on specific wing shape, flying style and wing loading, different seabird species have
52 different energetic costs associated with foraging considerable distances away from their colonies or
53 undertaking substantial migrations during the non-breeding period. Within seabirds, albatrosses are
54 well-adapted to gust-soaring which enables them to fly for hours without flapping their wings
55 (Richardson 2011; Sachs *et al.* 2012), whereas most smaller procellariiforms combine gust-soaring
56 with occasional wing-flapping (Spear & Ainley 1997b; Gibb *et al.* 2017). The required wind speed for
57 gust-soaring is species-specific and depends on the wing loading, and thus the total wing area and
58 body mass of the bird (Sachs 2005; Pennycuick 2008). If wind speeds are sufficiently high,
59 procellariiforms can fly against the wind without flapping their wings, typically following a more
60 tortuous track at lower average ground speed (i.e. speed of the bird flying over ground) than under
61 cross- or tailwinds (Sachs, Traugott & Holzapfel 2011). Nevertheless, flying against the wind causes
62 not only lower ground speeds (Wakefield *et al.* 2009) but also higher heart rates in wandering
63 albatrosses (*Diomedea exulans*), and is thus less efficient than flying under high ground speeds and
64 low energy expenditure with cross- or tailwinds (Weimerskirch *et al.* 2000). Similarly, Manx
65 shearwaters (*Puffinus puffinus*), were more likely to fly energy-efficiently by soaring under tailwinds
66 and crosswinds, but less so under headwinds (Gibb *et al.* 2017).

67 Favourable wind conditions are particularly important for seabirds during the breeding season, and
68 especially during chick-rearing, when adults regularly commute between foraging areas and
69 breeding colonies (Elliott & Gaston 2005). This is illustrated by stronger wind speeds enabling shorter
70 foraging trips and increased breeding success of wandering albatrosses at the Crozet Islands
71 (Weimerskirch *et al.* 2012). Most studies that investigated the interplay between wind and flight
72 behaviour in seabirds focussed on albatrosses, the largest gust-soaring species with the highest wing
73 loading. How winds affect the flight behaviour of smaller Procellariiforms like petrels and
74 shearwaters has been the focus of only few studies, most of which were based on visual
75 observations (Spear & Ainley 1997a; Spear & Ainley 1997b; but see Tarroux *et al.* 2016; Gibb *et al.*
76 2017). Better knowledge and understanding across more species and regions as to how seabirds
77 make use of winds and the energetic balance from this is necessary given the dramatic changes
78 expected for global wind patterns (IPCC 2019), which may be beneficial for some species
79 (Weimerskirch *et al.* 2012) but not others (Hass, Hyman & Semmens 2012). This is becoming
80 increasingly important since petrels and shearwaters are among the most threatened groups of
81 birds in the world (Dias *et al.* 2019).

82 The aim of this study was to investigate the flight behaviour of three sympatrically breeding
83 Antarctic fulmarine petrels in relation to local wind patterns. Cape petrels (*Daption capense*),
84 Antarctic petrels (*Thalassoica antarctica*) and southern fulmars (*Fulmarus glacialisoides*) are closely
85 related and belong to the family Procellariidae. They are characterized by flap-gliding flight (Spear &
86 Ainley 1997b), and reflect a gradient in average body mass, wing loading and aspect ratio (which
87 describes wing shape) (Table 1).

88 Coastal wind conditions in Antarctica are characterized by katabatic winds caused by cold air masses
89 flowing down from the Antarctic plateau and moving seawards, which interact with the easterly drift
90 of weather systems south of the Antarctic Divergence (Parish & Cassano 2003). During the summer
91 months, katabatic winds often show diurnal patterns, blowing stronger in the early morning hours

92 (Parish & Cassano 2003; Turner *et al.* 2009). This enables an investigation of strategies of seabirds as
93 to whether they avoid unfavourable wind conditions when commuting to and from their foraging
94 areas or alternatively, whether they are able to take advantage of particular wind conditions. A
95 recent study found high overlap in the timing of foraging and space use of the three species during
96 chick rearing, during which all three species foraged relatively close to their colony (maximum
97 distance from nest < 500 km; Dehnhard *et al.* 2020). While wind patterns in this area show a diurnal
98 pattern, light levels during the austral summer when these species are rearing their chicks allow
99 foraging over at least 20 hours each day (Dehnhard *et al.* 2020).

100 In detail, we aimed to test the following predictions:

- 101 1) Based on previous observational data on procellariiform seabirds including our study species
102 (Spear & Ainley 1997b), we predicted that birds will have higher ground speeds with higher wind
103 speeds under tailwinds but not under cross- or headwinds.
- 104 2) Between species, we expected morphology and particularly wing loading and aspect ratio to
105 affect average ground speeds and air speeds (i.e. speed of the bird relative to wind speed; at
106 constant ground speed, air speed increases with head- and decreases with tailwind). Species
107 with higher wing loading require higher air speeds and thus also higher wind speeds in order to
108 gust soar (Pennycuick 2008), but can then be expected to reach higher ground speeds under
109 higher wind speeds (cf. Wakefield *et al.* 2009). We therefore expected species to differ in their
110 response to increasing wind speeds resulting in different relationships between the birds'
111 ground speed and wind speed for each species. Based on the differences in wing loading and
112 aspect ratio, under tailwinds we expected Antarctic petrels to have the steepest increase in
113 ground speeds in response to wind speeds, followed by southern fulmars and last cape petrels.
114 We expected this response to be reversed or possibly absent under headwinds and crosswinds.
- 115 3) Within species, we expected a differential response of ground speed in relation to wind speed
116 between outbound and return commutes, since parental birds return with a meal for their chicks

117 and thus body mass and wing loading is higher on return than on outbound legs. We thus
118 predicted that under tailwinds, birds would show a steeper increase in ground speed in response
119 to wind speed on return legs compared to outbound legs, but to show an absence of this
120 relationship or possibly the opposite pattern under cross- and headwinds.

121 4) Based on 1) and knowledge from albatrosses (Weimerskirch *et al.* 2000), we expected species to
122 generally favour tailwinds and possibly crosswinds but avoid headwinds, both on outbound and
123 return commutes to/from foraging. We therefore expected (4.1) birds to adjust their flight
124 direction in relation to wind direction to avoid unfavourable strong headwinds and crosswinds
125 on both outbound and return legs and/or (4.2) to find a distinct daytime pattern in relation to
126 the diurnal wind pattern which had birds avoiding unfavourable winds. Finally (4.3), we expect
127 birds to limit their maximum distance from their nest when encountering headwinds on
128 outbound legs.

129

130

131 **Materials and Methods**

132 *Fieldwork*

133 Fieldwork was conducted in the Rauer Island group near Davis Research Station in the Prydz Bay
134 region, East Antarctica, during the austral summer 2015/16. We tracked breeding cape petrels,
135 Antarctic petrels and southern fulmars from two mixed colonies located in the north-west of Hop
136 Island within 2 km of each other (68.819°S, 77.689°E and 68.821°S, 77.678°E, respectively).

137 We used Sterna and Pica GPS loggers from Ecotone Telemetry (Gdynia, Poland), fitted with solar
138 panels and a remote download function as detailed in Dehnhard *et al.* (2020). During deployments,
139 birds were weighed (to the nearest 5 g, using spring scales), and we measured ½ wing span (using a
140 tape measure from the backbone to the wingtip, to the nearest 0.5 cm). We drew the outline of one
141 wing per bird on a paper to determine average wing area per species and calculate wing loading and

142 aspect ratio as described in Pennycuick (2008). The weight of the loggers with tape and glue was
143 below 2% of the birds' body mass. Most deployments were during the incubation stage (see
144 Dehnhard *et al.* 2020), but we here only included complete tracks from chick-rearing, i.e. 21 tracks of
145 8 Antarctic petrels, 79 trips of 8 cape petrels and 92 trips of 10 southern fulmars, tracked between
146 the 11th of January and the 12th of March.

147

148 *Treatment of data*

149 GPS loggers were programmed to record GPS positions at 15 minute intervals, and wet-dry data
150 (dive in/dive-out) every second. We interpolated positions when minor data gaps were present using
151 great circle distances of each bird to regular 15-min intervals. Ground speed was calculated based on
152 the great circle distance between two subsequent GPS fixes and flight direction of the birds was
153 calculated based the same two GPS fixes. We defined foraging trips to be those that exceeded a
154 distance of 10 km from the nest and contained dive data. Trips were divided into outbound, middle
155 and return legs, following the methodology of Wakefield *et al.* (2009). Briefly, thresholds for
156 outbound, middle and return legs of foraging trips were determined on the population level based
157 on maximum distance reached and the proportion of the total trip time. Since the focus of our study
158 was on the commuting part, we focussed on the outbound and return legs and excluded middle
159 sections and any periods when birds were foraging or resting and not commuting (see Supplement 1
160 for details).

161 We extracted the times for sunrise, sunset, nautical dusk and nautical dawn (when the sun is 12°
162 below the horizon) for each of the birds' GPS positions in the R-package *maptools* (Bivand & Lewin-
163 Koh, 2016) to determine light levels experienced by the birds during their foraging trips.

164 Wind speed and direction at 10m height was extracted from gridded forecast data (Antarctic
165 Mesoscale Prediction System (AMPS) Polar Weather and Research Forecasting (Polar WRF) model

166 version 3.7.1 (Bromwich *et al.* 2013) with 3-hour by 10 km horizontal resolution;
167 http://www2.mmm.ucar.edu/rt/amps/wrf_grib/) and matched in time and space to the GPS position
168 data of the birds using *raadtools* (Sumner 2017). Polar WRF provides higher resolution than current
169 meteorological reanalyses and performs adequately in evaluating surface wind in the Antarctic
170 (Bromwich *et al.* 2013). As in Tarroux *et al.* (2016), we used forecast data 12 hours after each
171 analysis to allow the model to adequately equilibrate with the analysis cycle.

172 We calculated the absolute difference between the birds' flight direction and wind direction
173 (hereafter: $\Delta\text{Dir}_{\text{fw}}$) which was on a scale from 0° to 180°. Since wind direction is defined as the
174 direction from which the wind is coming, while flight direction is the direction into which the bird is
175 flying, $\Delta\text{Dir}_{\text{fw}}$ is at 90° if a bird is flying perpendicular to the wind (i.e. crosswind), decreasing if the
176 bird is flying against the wind (with maximum headwind at 0°) and increasing if a bird is flying with
177 the wind (maximum tailwind at 180°). To compare wind conditions that the birds experienced at sea
178 on their foraging trips with those near their breeding colony, we obtained hourly wind speed and
179 wind direction data from the two nearest weather stations, i.e. Davis Research Station (68.577° S,
180 77.968° E; 30 km north-northeast of Hop Island) and Zhong Shan Station (69.374° S, 76.372° E; 80 km
181 south-southwest of Hop Island).

182

183 *Statistics*

184 All statistical procedures were run in R version 3.6.1 (R Core Team 2019). Linear mixed models
185 (LMMs) to test predictions 1-3 were run in the R-package *lme4* (Bates, Maechler & Bolker 2011) and
186 p-values were computed in *lmerTest* (Kuznetsova, Brockhoff & Christensen 2014). Interaction terms
187 were illustrated using the R-package *interactions* (Long 2019). Where appropriate, post-hoc tests
188 based on pairwise comparisons of least square means (LSM) were performed in the *lsmeans* package
189 (version: 2.30-0; Lenth 2016) using Tukey's method for p-value adjustment.

190 Generalized additive mixed models (GAMMs) to test prediction 4 were run in the R-package *mgcv*
191 (version 1.8-3.1; Wood 2016). Model assumptions for LMMs and GAMMs were validated using the
192 protocols described in Zuur et al. (2009) and Wood (2017). Significance level was $p = 0.05$.

193 To test predictions 1, 2 and 3, i.e. whether ground speeds are affected by wind speed, wind direction
194 relative to flight direction, differ between species and trip sections (two-level factor: outbound or
195 return leg), we set up a LMM with ground speed as the dependent variable and wind speed
196 (continuous), $\Delta\text{Dir}_{\text{fw}}$ (continuous), species (factor) and trip section (factor) as well as all possible 2-
197 way, 3-way and the 4-way interactions as explanatory variables. The 4-way interaction term
198 between wind speed, $\Delta\text{Dir}_{\text{fw}}$, species and trip section was significant (see Results). To test predictions
199 1 and 2, we therefore split the dataset by species and by $\Delta\text{Dir}_{\text{fw}}$, thereby transforming $\Delta\text{Dir}_{\text{fw}}$ into
200 three categories, with $0^\circ \geq \Delta\text{Dir}_{\text{fw}} \leq 60^\circ$ being headwind, $60^\circ \geq \Delta\text{Dir}_{\text{fw}} \leq 120^\circ$ being crosswind and 120°
201 $\geq \Delta\text{Dir}_{\text{fw}} \leq 180^\circ$ being tailwind (**hereafter: wind categories**). To test prediction 3, we tested
202 separately for species and tailwinds, crosswinds and headwinds (again as categories) whether trip
203 section and particularly the interaction between trip section and wind speed had an influence on
204 ground speed.

205

206 To test prediction 4.1, we investigated if birds adjusted their flight direction in response to wind
207 direction and wind speed and tested for differences between species and trip sections. We thus ran
208 a LMM with $\Delta\text{Dir}_{\text{fw}}$ as dependent variable, species, trip section and wind speed as explanatory
209 variables, as well as all possible 2- and 3-way interaction terms. As previously, we included trip
210 nested within BirdID as random factors and subsequently simplified the model by removing non-
211 significant interaction terms and/or continued the analyses by splitting the dataset by species and
212 trip section.

213 To test prediction 4.2, we investigated if outbound and return sections of foraging trips were
214 uniformly distributed over the course of the day and if birds encountered headwinds, crosswinds
215 and tailwinds uniformly over the day. Since time of day is a circular variable, we used GAMMs to test
216 this relationship and calculated the number of time stamps for outbound or return legs and the wind
217 category (headwind, tailwind, crosswind) for each hour of the day for each bird. The dependent
218 variable thus consisted of count data (equivalent to a histogram). We summed up the number per
219 BirdID instead of trip, since at maximum 4 locations per hour could belong to the same trip (loggers
220 were programmed to collect GPS data at 15 min intervals) and the amount of variation between
221 trips of the same individual was therefore low.

222 Species, trip section and wind category were included as explanatory variables into the global
223 GAMM, together with all possible 2- way and the 3-way interactions. We further included hour of
224 the day (with a tensor product smoother accounting for circularity) and also the interaction terms
225 between hour of day and species, hour of day and trip section as well as hour of day and wind
226 category (as tensor product interactions). BirdID was included as random effect. We initially set the
227 maximum number of knots to 5 in order to avoid overfitting, and used the function `gam.check` to
228 check whether models with more knots had a better fit. GAMMs were run on a poisson distribution
229 (since the dependent variable was a count). Since all three two-way interactions between hour of
230 day turned out to be significant (see Results), we subsequently split the dataset by species.

231 Finally, to test prediction 4.3, we investigated if maximum distance from nest was affected by the
232 average difference between the wind direction and the birds' flight direction ($\Delta\text{Dir}_{\text{fw}}$) across the
233 outbound trip, using linear mixed models. Our dataset therefore consisted of only one datapoint per
234 trip. Maximum distance from nest was included as dependent variable, species and average $\Delta\text{Dir}_{\text{fw}}$
235 on the outbound trip section as explanatory variables, together with the 2-way interaction term.
236 BirdID was included as random factor.

237 **Results**

238 *Wind conditions at the coast and encountered on foraging trips*

239 Predominant wind direction in the coastal area around the breeding site was from the north-east to
240 east. Wind speeds peaked in the early morning and were lowest at midday (Fig. 1). On their
241 commute to foraging areas, birds experienced mostly easterly winds (Fig. 2). During outbound legs,
242 birds of all three species headed into north-westerly to north-easterly directions, while flight
243 directions were south to south-west during return legs (Fig. 2, Supplement 2). The majority of
244 foraging trips described a loop in clock-wise direction, in which case birds flew eastwards during the
245 middle section (Supplement 3). This pattern was more distinct for Antarctic petrels (19 out of 21
246 foraging trips) than for the other two species (50 out of 79 foraging trips of cape petrels and 58 out
247 of 91 foraging trips of southern fulmars, respectively).

248

249 *Ground speed in relation to wind speed, ΔDir_{fw} , species and trip section*

250 Ground speed was significantly affected by the 4-way interaction between wind speed, wind
251 direction relative to flight direction (ΔDir_{fw}), species and trip section (Table 2, Model M1_full).

252 Testing **prediction 1** (birds should have higher ground speeds with higher wind speeds under
253 tailwinds but not under cross- or headwinds), the interaction between wind speed and ΔDir_{fw} was
254 significant for all three species (Table 2, Models 2.1 to 2.3). Ground speed increased in all three
255 species with increasing ΔDir_{fw} and thus an increasing tailwind component (Fig. 3). In agreement with
256 prediction 1, ground speed increased with increasing wind speed in all three species under tailwind,
257 while the opposite was true for headwinds (Figs. 3 and 4, Table 2; Models 3.1.1 to 3.1.3 and 3.3.1 to
258 3.3.3). Also in agreement with prediction 1, wind speed had no significant effect on ground speed
259 under crosswinds (Fig. 4b, Table 2; Model 3.2_red).

260 In agreement with **prediction 2** (morphology and particularly wing loading should affect average
261 ground speeds of the three species), we found significant interaction terms between species and
262 wind speed for both tailwind and headwind on the birds' ground speed (Fig. 4; Models 3.1 and 3.3),
263 indicating a species-specific response to different wind speeds. Under crosswinds, ground speed
264 differed significantly between species, but the interaction between wind speed and species was not
265 statistically significant (Fig. 4b, Models 3.2 and 3.2_red). Antarctic petrels had higher average ground
266 speeds than southern fulmars under tailwind (LSM; $t = 3.33$, $p = 0.005$), and they visually showed a
267 steeper increase in ground speed under increasing wind speeds than the other two species (Fig 4a),
268 thus matching prediction 2. However, contrasting prediction 2, cape petrels (the species with the
269 lowest wing loading), had intermediate ground speed levels and did, not for average wind speed,
270 differ significantly from either southern fulmars or Antarctic petrels under tailwinds (LSM ; $t \leq |$
271 $2.29|$, $p \geq 0.089$; Fig. 4a). Also under headwinds, cape petrels and southern fulmars visually showed
272 a very similar decrease in ground speed in response to increasing wind speeds, while Antarctic
273 petrels showed – agreeing with prediction 2 – the strongest response (Fig. 4c).

274 Returning to the 3-way interaction between wind speed, ΔDir_{fw} and trip section, the interaction
275 between wind speed and trip section was significant for all three species under tailwinds (Table 2,
276 Models 4.1-4.3). Matching **prediction 3** (the response of ground speed in relation to wind speed
277 should differ between outbound and return commutes), ground speed increased for all three species
278 with a steeper slope for outbound than for return trip sections (Figures 5a-5c). Under crosswinds,
279 the interaction term between trip section and wind speed was significant only for cape petrels and
280 southern fulmars but not Antarctic petrels (Models 5.1-5.3). The direction of the relationship was
281 reversed between southern fulmars and cape petrels, while Antarctic petrels reached generally
282 higher ground speeds on return than outbound trip sections (Figures 5d-5f). Finally, under
283 headwinds, interaction terms between trip section and wind speed were non-significant for all three
284 species (Models 6.1-6.3; Fig. 5g-5i). Cape petrels and southern fulmars reached higher ground

285 speeds on return compared to outbound legs, while there was no significant difference for Antarctic
286 petrels (Models 6.1_red-6.3_red).

287

288 *Flight direction, timing of commute and maximum distance to colony in relation to wind conditions*

289 Flight direction relative to wind direction ($\Delta\text{Dir}_{\text{fw}}$) was significantly affected by the three-way
290 interaction between wind speed, species and trip section (Table 3, Model mp2.1_full). Cape petrels
291 and Antarctic petrels experienced on average smaller angles between flight direction and wind
292 direction (i.e. smaller $\Delta\text{Dir}_{\text{fw}}$), and thus more headwinds, on their outbound compared to return legs
293 (LSM; $t > |7.99|$, $p < 0.001$), while it was the opposite for southern fulmars (LSM; $t = 2.73$, $p = 0.006$;
294 Fig. 6). Split by species, the interaction between wind speed and trip section was significant in all
295 three species (Table 3, Models mp2_2.1, mp2_2.2 and mp2_2.3). In agreement with **prediction 4.1**
296 (species should adjust their flight direction in relation to wind direction to avoid unfavourable strong
297 headwinds and crosswinds), $\Delta\text{Dir}_{\text{fw}}$ and thus the tailwind component increased with increasing wind
298 speeds on outbound legs of cape petrels (mp2_2.1.1; Fig. 6). However, on return legs, this
299 relationship was missing for cape petrels (mp2_2.1.2; Fig. 6). For Antarctic petrels and southern
300 fulmars, the tailwind component increased with increasing wind speeds on return legs (Table 3,
301 Model mp2_2.2.2 & mp2_2.3.2, Fig. 6), but not on outbound legs (Table 3, models mp2_2.2.1 and
302 mp2_2.3.1; Fig. 6).

303 GAMMs to test **prediction 4.2** (commuting trips should show a distinct daytime pattern in relation to
304 the diurnal wind patterns so that birds would avoid unfavourable winds) reflected that outbound
305 and return legs were not uniformly distributed across the light hours, except for outbound legs of
306 Antarctic petrels (Fig. 7). The timing of outbound and return legs differed between species
307 (significant 2-way interaction terms between species as well as trip section with time of day; Table 3,
308 gamm1_full; Fig. 7). The probability of cape petrels and southern fulmars to be on outbound legs

309 appeared to visually match the hours of the day with higher wind speeds. The timing of return legs
310 coarsely matched the hours of the day with the lowest wind speeds in all three species, despite
311 inter-specific differences in this trait (Fig. 7). Birds experienced headwinds, tailwinds or crosswinds at
312 different times of the day (significant 2-way interaction between wind category and time of day;
313 Table 3; gamm1_full ; Fig. 8). All three species experienced headwinds mostly over midday and in the
314 afternoon, and thus in the hours of the day when coastal katabatic winds are typically lowest.
315 Crosswinds were experienced by cape petrels and Antarctic petrels mostly in the early morning
316 hours, coinciding with the time when coastal katabatic winds are typically strongest. Southern
317 fulmars showed no distinct daytime pattern for encountering crosswinds and cape petrels for
318 encountering tailwinds (Fig. 8). Similarly, the probability of Antarctic petrels to encounter tailwinds
319 was only marginally increased during the late morning and midday hours, thus coinciding with low
320 katabatic winds. Southern fulmars, however, encountered tailwinds mostly in the early morning and
321 late evening hours, and thus during the hours with strong katabatics.

322 Finally, average $\Delta\text{Dir}_{\text{w}}$ on outbound legs had no significant effect on the maximum distance from
323 nest that birds reached on foraging trips (Table 3, models mp2_3_full and mp2_3_red). This result
324 contradicted **prediction 4.3**, under which we expected birds to limit their trip distance when
325 encountering headwinds on the outbound leg.

326

327

328 **Discussion**

329 *Ground speed in relation to wind speed and differences within and between species*

330 In agreement with our prediction 1, ground speeds in all three species increased with wind speed
331 under tailwinds, but decreased under head winds, which matches previous observations in fulmarine
332 petrels and albatrosses (Spear & Ainley 1997b; Wakefield *et al.* 2009). Antarctic petrels, and thus the
333 species with the highest wing loading, showed the steepest response of ground speed in response to

334 wind speeds, matching prediction 2. We had further expected that cape petrels, the species with the
335 lowest wing loading, lowest body mass and lowest aspect ratio, would show the gentlest response in
336 ground speed in response to wind speed among the three species, but instead cape petrels turned
337 out to be intermediate between Antarctic petrels and southern fulmars. This is an interesting result
338 and may highlight the importance of other morphological or behavioural aspects besides wing
339 loading and aspect ratio for flight behaviour and utilization of winds. Among the three study species,
340 southern fulmars had the highest body mass but showed intermediate wing loading and also
341 intermediate aspect ratios (Table 1). This was due to the wing area of southern fulmars being
342 comparatively larger, due to a wider wing span and broader wings (i.e. longer primary and secondary
343 feathers) compared to Antarctic petrels (unpublished data), resulting in the lower wing loading and
344 aspect ratio of southern fulmars compared to Antarctic petrels. We have no evidence from
345 observations that southern fulmars would fly differently under head or tailwinds than the other two
346 species (e.g. use flapping flight in a different way), yet this could be a possible explanation for our
347 findings.

348 Within species, we found that under tailwinds, ground speed increased stronger with wind speed on
349 return than on outbound legs, matching our prediction (3) that the increased body mass due to
350 successful foraging should affect wing loading and thus flight characteristics. This finding also means
351 that the benefit from tailwinds might be highest on return legs, and thus agrees with earlier findings
352 that the ideal location of a colony would be downwind from feeding areas (Pennycuick 1989; Spear
353 & Ainley 1997a; Tarrowx *et al.* 2016). In Antarctica, ice-free land that is suitable for breeding is
354 limited and thus this ideal condition might be difficult to achieve. For example, where ice-free areas
355 near the coast is lacking, Antarctic petrels may breed on nunataks located up to 200 km inland, and
356 face unfavourably strong crosswinds on their commute over land (Tarrowx *et al.* 2016). Also in our
357 study system of coastal breeding fulmarine petrels, the birds mostly encountered crosswinds – both
358 on outbound and return legs of foraging trips (cf. Fig. 2 and Supplement 2). Conspicuously, many
359 foraging trips described a loop in clockwise-direction, i.e. birds flying out in northerly to north-

360 westerly direction, heading eastwards on the middle section of the foraging trip and returning in
361 south to south-westerly direction towards the colony (Supplements 2 and 3). Given the predominant
362 easterly winds, this implies birds to predominantly face headwinds on the middle (foraging) section
363 of foraging trips, but crosswinds during outbound and return legs. This loop pattern may be
364 beneficial for the commuting part, while they likely encountered headwinds during the middle
365 section which could reduce flight speed but possibly enhance prey detection: Procellariiforms are
366 olfactory foragers (Nevitt 1999; Nevitt, Reid & Trathan 2004) and thus flying into headwinds during
367 fine-scale search for food may be beneficial (Nevitt, Losekoot & Weimerskirch 2008).

368

369 *Adjustment of timing of commutes, flight direction and distance from colony to wind conditions*

370 Given the significant positive effect of tailwinds on the birds' ground speeds, and the observed
371 negative impact under headwinds, we expected birds to adjust their flight direction, timing of
372 commutes to/from foraging locations and/or the maximum distance from nest to ambient wind
373 conditions (predictions 4.1 – 4.3). Overall, we found mixed evidence for these predictions. There was
374 no consistency among species to adjust their flight direction in response to unfavourable strong
375 headwinds (prediction 4.1), neither on outbound nor on return legs. Thus, Antarctic fulmarine
376 petrels did not adjust their course and thus possibly their foraging location(s) to prevailing wind
377 conditions. Birds also did not adjust the maximum distance from the nest, and thus their commute
378 distance, to the encountered wind directions on outbound legs (prediction 4.3). Both of these results
379 can be explained by the need of parental birds to provision chicks with sufficient food at regular
380 intervals. Shortening the foraging trip or adjusting the flight direction to avoid headwinds may result
381 in birds visiting less productive foraging areas, which in turn might increase foraging costs and
382 reduce foraging success (sensu optimal foraging theory; MacArthur & Pianka 1966). This may further
383 cause a reduced provision rate to the chick and affect breeding success and life-time reproductive
384 success (Sæther *et al.* 1997; Lescroël *et al.* 2010). Previous studies in seabirds have highlighted that

385 parental birds will — within their physiological limits — adapt foraging locations and extend trip
386 distances substantially to provision their chicks in years with low local food availability (Burke &
387 Montevecchi 2009; Montevecchi *et al.* 2009; Dehnhard *et al.* 2016). Given the energetic costs for
388 flight in fulmarine petrels are among the lowest compared to other (sea-)bird species (Pennycuik
389 2002; 2008), the costs for flying a longer distance, possibly even against the wind, will be
390 outweighed easily if the feeding grounds are productive. As such, flying against the wind for one part
391 of the foraging trip comes at a lower cost for a breeding bird than to risk the breeding success and
392 thus all previous investment into the breeding season. One could expect, though, that birds during
393 the non-breeding period would be less constrained and adapt their flight direction to wind direction
394 more flexibly, which indeed has been demonstrated in wandering albatrosses (Weimerskirch *et al.*
395 1993).

396 Although the three species of fulmarine petrels showed differences in the timing of outbound and
397 return trips, there was a general tendency in cape petrels and southern fulmars towards outbound
398 legs to occur in the early morning hours and afternoon/evening hours when katabatic winds were
399 stronger than during midday. In contrast, return trips in all three species occurred mostly between
400 the late morning and early evening hours, and thus under lower katabatic winds. Remarkably, this
401 same time period (i.e. late morning to early evening hours), and thus low coastal katabatic winds,
402 coincided with birds encountering most headwinds. Crosswinds, in contrast, were encountered by
403 cape and Antarctic petrels mostly in the early mornings and late evenings – and thus matching
404 coarsely the timing of the outbound trips – and of the stronger katabatic winds. Finally, southern
405 fulmars encountered tailwinds mostly during early mornings and late evenings and thus again
406 coinciding with stronger katabatics. To summarize, our data strongly indicates that commuting legs
407 and the encounter of head-, cross- and tailwinds over the course of the day did not happen at
408 random, but showed some diurnal patterns (with few exceptions, namely outbound trips of Antarctic
409 petrels, encounters of crosswinds by southern fulmars and tailwinds by cape petrels). Our data
410 further suggests that fulmarine petrels adjust the timing of their outbound and return legs in a way

411 to encounter headwinds when katabatic winds tend to be weak but crosswinds or tailwinds when
412 katabatic winds are strong. These results are therefore in support of our prediction that birds would
413 adjust their timing of commutes to either benefit from katabatic winds (under cross- and tailwinds
414 on return commutes) or to avoid headwinds (on outbound commutes) (prediction 4.2). Despite this
415 supposed adjustment, we observed individuals of all three species encountering the full range from
416 weak to strong head-, cross- and tailwinds (Fig 2). Naturally, katabatic winds prevail at the coast and
417 get weaker further out at sea, but also get disrupted by weather systems (Parish & Cassano 2003).
418 This is also why we used weather model-derived wind data at sea to assess the birds flight
419 behaviour. Thus, although birds may adjust their commuting times to katabatic winds, this does not
420 always work out for them, particularly under a passing storm.

421

422 *Variability and trends in wind conditions*

423 Like other species at high latitudes, Antarctic fulmarine petrels have evidently adapted to particular
424 environmental conditions which are potentially finely balanced due to the apparent sensitivity of
425 polar climate to anthropogenic change (Clucas *et al.* 2014; Descamps *et al.* 2017). The strength and
426 variability of the near surface winds and their interaction with the katabatic flow is therefore
427 relevant in considering whether the energetics of the birds are being positively or negatively
428 impacted under recent conditions, and how this will play out into the future. Based on ERA5
429 reanalysis data from 1979-2019, the linear trends of near-surface (10 m elevation) wind speed in our
430 study region have been overall stable (Supplement 4, Fig. S3.1). There is no evidence over the last 4
431 decades for trends or the influence of the Southern Annular Mode (SAM) on the monthly mean wind
432 speed for the summer breeding season. However, based on CMIP6 simulations for future wind
433 patterns in the foraging area of our study populations, easterly winds will generally prevail at similar
434 levels as currently, while the influence of southerly winds will get weaker (Supplement 4, Fig. S3.2).
435 For our study populations, this might imply less headwinds on return journeys from foraging, but

436 hinder departures. To better assess likely impacts on the bird populations in our study area in long-
437 term trends and inter-annual variability, further use of detailed regional climate modelling is
438 required.

439

440

441 **Conclusions**

442 We demonstrated the effect of wind speeds and wind direction on the ground speeds of three
443 species of fulmarine petrels on their commutes to and from foraging areas. Our results emphasize
444 the importance of winds for this group of gust-soaring seabirds, but also highlight differences
445 between species, some of which cannot be explained by morphological differences in wing loading
446 and aspect ratio. While all three species benefitted from tailwinds, birds did not adjust their flight
447 paths to the prevailing wind directions. However, our data suggested that birds adjusted the timing
448 of outbound and return commutes to the diurnal katabatic winds in order to avoid strong headwinds
449 and benefit from tailwinds and possibly crosswinds.

450 Our results are highly relevant in the context of a changing environment. While winds are necessary
451 for the energy-efficient gust-soaring flight style of Antarctic fulmarine petrels, any significant future
452 changes in the diurnal katabatic wind patterns might cause birds to face unfavourably strong
453 headwinds more frequently and thus increase foraging costs. This could ultimately impact breeding
454 success and population trajectories, although the extent of this impact is difficult to estimate and
455 requires further characterisation of the trends and variability in diurnal winds using modelling that
456 well-captures the features of the Antarctic katabatic flow.

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473

474 **Authors' contributions**

475 All authors conceived the ideas and designed the study. ND and LE conducted the fieldwork. LE and
476 AK processed the environmental covariate data. ND analysed the data and led the writing of the
477 manuscript. All authors contributed to the writing of the paper and gave final approval for
478 publication.
479

480 **Data availability statement**

481 Biologging data are publically available through the Australian Antarctic Data Centre:
482 [https://data.aad.gov.au/metadata/records/AAS_4087_Fulmarine_petrel_tracking_study_Hop_Island_2](https://data.aad.gov.au/metadata/records/AAS_4087_Fulmarine_petrel_tracking_study_Hop_Island_2015_16)
483 [015_16](https://data.aad.gov.au/metadata/records/AAS_4087_Fulmarine_petrel_tracking_study_Hop_Island_2015_16)
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615 **Table 1.** Average (\pm S.D.) body mass, wing span, wing area and resulting aspect ratio and wing
616 loading for Antarctic petrels, cape petrels and southern fulmars at Hop Island, Antarctica. All birds
617 were measured and weighed during the breeding season.

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619

	Body mass in g	Wing span in cm	Wing area in cm ²	Wing loading in kg/m ²	Aspect ratio	N
Cape petrel	469 \pm 48	93 \pm 3	762 \pm 80	6.24 \pm 0.99	11.31 \pm 0.88	15
Antarctic petrel	714 \pm 71	106 \pm 4	957 \pm 79	7.51 \pm 0.95	11.86 \pm 0.69	31
Southern fulmar	783 \pm 85	116 \pm 4	1173 \pm 91	6.65 \pm 0.94	11.61 \pm 0.76	25

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622 Table 2. Outcomes of linear mixed models (LMMs) investigating the effects of wind speed, wind direction relative to flight direction (ΔDir_{fw}), species and trip
623 section on ground speed (as dependent variable in all models). Starting with the initial full model (m1_full), models were reduced in complexity and the
624 dataset split to investigate the effects in detail and test predictions 1, 2 and 3 (see Methods). Significant effects are marked in bold, test statistics refer to
625 the variables marked in red in the main model. N = positions for Antarctic petrels, cape petrels and Southern fulmars, respectively.

Model Name	Explanatory variables	Interaction terms	Data	Test statistic for variables marked in red
m1_full	wind speed + ΔDir_{fw} + species + trip section	all possible 2-way interactions + and 3-way interactions + wind speed * ΔDir_{fw} * species * trip section	all	$F_2 = 11.58, p < 0.001$
Testing Prediction 1				
m2.1	wind speed + ΔDir_{fw}	wind speed * ΔDir_{fw}	Cape petrel	$F_1 = 505.56, p < 0.001$
m2.2	wind speed + ΔDir_{fw}	wind speed * ΔDir_{fw}	Antarctic petrel	$F_1 = 75.44, p < 0.001$
m2.3	wind speed + ΔDir_{fw}	wind speed * ΔDir_{fw}	Southern Fulmar	$F_1 = 24.99, p < 0.001$
Testing Prediction 2				
m3.1	wind speed + species	wind speed * species	Tailwind	$F_2 = 12.64, p < 0.001$
m3.1.1	wind speed		Tailwind Cape petrels	$F_1 = 151.17, p < 0.001$
m3.1.2	wind speed		Tailwind Antarctic petrels	$F_1 = 18.48, p < 0.001$
m3.1.3	wind speed		Tailwind Southern fulmars	$F_1 = 7.41, p = 0.007$
m3.2	wind speed + species	wind speed * species	Crosswind	$F_2 = 1.49, p = 0.225$
m3.2_red	wind speed + species		Crosswind	$F_1 = 1.02, p = 0.312; F_2 = 3.94, p = 0.036$
m3.3	wind speed + species	wind speed * species	Headwind	$F_2 = 15.60, p < 0.001$
m3.3.1	wind speed		Headwind Cape petrels	$F_1 = 71.75, p < 0.001$
m3.3.2	wind speed		Headwind Antarctic petrels	$F_1 = 34.94, p < 0.001$
m3.3.3	wind speed		Headwind Southern fulmars	$F_1 = 26.10, p < 0.001$
Testing Prediction 3				
m4.1	wind speed + trip section	wind speed * trip section	Tailwind Cape petrels	$F_1 = 18.74, p < 0.001$
m4.2	wind speed + trip section	wind speed * trip section	Tailwind Antarctic petrels	$F_1 = 8.95, p = 0.003$
m4.3	wind speed + trip section	wind speed * trip section	Tailwind Southern fulmars	$F_1 = 4.56, p = 0.033$
m5.1	wind speed + trip section	wind speed * trip section	Crosswind Cape petrels	$F_1 = 7.43, p = 0.006$
m5.2	wind speed + trip section	wind speed * trip section	Crosswind Antarctic petrels	$F_1 < 0.01, p = 0.975$
m5.2_red	wind speed + trip section		Crosswind Antarctic petrels	$F_1 = 2.41, p = 0.122; F_1 = 5.67, p = 0.018$
m5.3	wind speed + trip section	wind speed * trip section	Crosswind Southern fulmars	$F_1 = 6.76, p = 0.009$
m6.1	wind speed + trip section	wind speed * trip section	Headwind Cape petrels	$F_1 = 0.64, p = 0.426$
m6.1_red	wind speed + trip section		Headwind Cape petrels	$F_1 = 79.71, p < 0.001; F_1 = 52.42, p < 0.001$
m6.2	wind speed + trip section	wind speed * trip section	Headwind Antarctic petrels	$F_1 = 0.13, p = 0.722$
m6.2_red	wind speed + trip section		Headwind Antarctic petrels	$F_1 = 29.17, p < 0.001; F_1 = 2.73, p = 0.103$
m6.3	wind speed + trip section	wind speed * trip section	Headwind Southern fulmars	$F_1 = 2.11, p = 0.147$
m6.3_red	wind speed + trip section		Headwind Southern fulmars	$F_1 = 23.98, p < 0.001; F_1 = 20.65, p < 0.001$

627 Table 3. Modelling approach to test prediction 4, which consisted of three steps. In the first step (upper part of the table), we ran linear mixed models
628 (LMMs) with $\Delta\text{Dir}_{\text{fw}}$ as dependent variable. Models were based on the same dataset as those detailed in Table 1, with identical sample sizes. In the second
629 step (middle part of the table), we ran generalized additive mixed models (GAMMs) which were based on the number of data per hour and bird identified
630 as commuting (as detailed in the Methods). The dependent variable was thus a count (ranging from 0-33 per hour and BirdID). Hour of day was included as
631 circular smoothed term. N = 3768 observations in total. In the third step (bottom part of the table) we once more used linear mixed models to explore if
632 maximum distance from nest (as dependent variable) was affected by average $\Delta\text{Dir}_{\text{fw}}$ on the outbound section of the foraging trip. BirdID was included as
633 random effect. N= 196, with N = 1 per trip.

634

Model Name	Explanatory variables	Interaction terms	Data	Test statistic for variables marked in red
LMMs with $\Delta\text{Dir}_{\text{fw}}$ as dependent variable				
mp2_1_full	wind speed + species + trip section	all possible 2-way interactions + wind speed*species*tripsection	all	F₂ = 17.38, p < 0.001
mp2_2.1	wind speed + trip section	windspeed*tripsection	Cape petrel	F₁ = 136.36, p < 0.001
mp2_2.1.1	wind speed		Cape petrel Outbound legs	F₁ = 5.58, p = 0.018
mp2_2.1.2	wind speed		Cape petrel Return legs	F ₁ = 2.16, p = 0.142
mp2_2.2	wind speed + trip section	windspeed*tripsection	Antarctic petrel	F₁ = 7.70, p = 0.006
mp2_2.2.1	wind speed		Antarctic petrel Outbound legs	F ₁ = 1.30, p = 0.256
mp2_2.2.2	wind speed		Antarctic petrel Return legs	F₁ = 47.63, p < 0.001
mp2_2.3	wind speed + trip section	windspeed*tripsection	Southern fulmar	F₁ = 17.01, p < 0.001
mp2_2.3.1	wind speed		Southern fulmar Outbound legs	F ₁ < 0.01, p = 0.951
mp2_2.3.2	wind speed		Southern fulmar Return legs	F₁ = 20.13, p < 0.001
GAMMs with count data as dependent variable				
gamm1_full	species + trip section + wind category + s(Hour of day)	species*trip section + species*wind category + wind category*trip section + species*trip section*wind category + s(Hour)*species + s(Hour)*trip section + s(Hour)*wind category	all_count data	Dev = -93.49, p < 0.001; Dev = -661.85, p < 0.001; Dev = -199.09, p < 0.001
gamm2	trip section + wind category + s(Hour of day)	wind category*trip section + s(Hour)*trip section + s(Hour)*wind category	Cape Petrel	Dev = -149.49, p < 0.001; Dev = -149.74, p < 0.001
gamm3	trip section + wind category + s(Hour of day)	wind category*trip section + s(Hour)*trip section + s(Hour)*wind	Antarctic Petrel	Dev = -5.53, p = 0.050; Dev = -19.86, p = 0.004

gamm4	trip section + wind category + s(Hour of day)	category wind category*trip section + s(Hour)*trip section + s(Hour)*wind category	Southern Fulmar	Dev = -703.57, p < 0.001; Dev = -150.53, p < 0.001
LMMs with Maximum distance from nest as dependent variable				
mp2_3_full	species + ΔDir_{fw} (average over outbound trip section)	species*ΔDir_{fw} (averaged over outbound section for each trip)	all	$F_2=0.06, p = 0.940$
mp2_3_red	species + ΔDir_{fw} (average over outbound trip section)		all	$F_2 = 19.53, p < 0.001$; $F_1 = 3.54, p = 0.061$

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644 Figure 1. Plot showing wind speed over the course of the day (left) and the predominating wind
645 direction (right) at Davis Research station (located 30 km north-northeast of Hop Island) and Zhong
646 Shan station (located 80 km south-southwest from Hop Island) during the study period (11th of
647 January to 11th of March 2016).

648

649 Figure 2. Circular histograms of flight direction of Antarctic petrels, cape petrels and southern
650 fulmars and experienced wind direction on outbound and return sections of foraging trips.

651

652 Figure 3. Birds' ground speeds in response to the difference between the wind direction and the
653 birds' flight direction ($\Delta\text{Dir}_{\text{fw}}$) for different wind speeds. Plots are based on models m2.1, m2.2 and
654 m2.3 (Table 2). Solid lines reflect the significant interaction effects between wind speed and $\Delta\text{Dir}_{\text{fw}}$. N
655 = 832 data points for Antarctic petrels, 2972 for cape petrels and 2661 for southern fulmars,
656 respectively.

657

658 Figure 4. Species differences in ground speed in response to wind speed under tail-, cross- and
659 headwind in Antarctic petrels, cape petrels and southern fulmars. Interaction effects between
660 species and wind speed are illustrated with solid lines when significant, and dashed lines when non-
661 significant. Plots are based on models m3.1, m3.2 and m3.3 (Table 2).

662

663 Figure 5. Ground speed in response to wind speed under tail-, cross- and headwind and separately
664 for outbound and return sections of foraging trips in Antarctic petrels, cape petrels and southern
665 fulmars. Plots are based on models m4.1-m4.3, m5.1-m5.3 and m6.1-m6.3 (Table 2). Interaction
666 effects between trip sections and wind speed are illustrated with solid lines when significant, and
667 dashed lines when non-significant.

668

669 Figure 6. Flight direction relative to wind direction ($\Delta\text{Dir}_{\text{fw}}$) for outbound and return journeys in
670 response to wind speed under tail-, cross- and headwinds. Plots are based on models mp2_2.1,
671 mp2_2.2 and mp2_2.3 (Table 2). Lines represent interaction effects between trip sections and wind
672 speed. Solid lines represent a significant relationship between wind speed and $\Delta\text{Dir}_{\text{fw}}$, dashed a non-
673 significant relationship.

674

675 Figure 7. Outputs of Generalized additive mixed models (gamm2-4; see Table 3) illustrating the
676 significant interaction effects between time of day and trip section (outbound versus return legs) on
677 the number of birds commuting per hour. Models were run separately for cape petrels, Antarctic
678 petrels and southern fulmars. Light grey background reflects maximum twilight times, and dark grey
679 background reflects maximum periods of darkness (only experienced by southern fulmars at the end
680 of the chick-rearing period).

681 Figure 8. Outputs of Generalized additive mixed models (gamm2-4; see Table 3) illustrating the
682 significant interaction effects between time of day and wind category (i.e. headwind, crosswind and
683 tailwind) on the number of birds commuting per hour. Models were run separately for cape petrels,
684 Antarctic petrels and southern fulmars. Light grey background reflects maximum twilight times, and
685 dark grey background reflects maximum periods of darkness (only experienced by southern fulmars
686 at the end of the chick-rearing period).