Coping with the commute: Behavioural responses to wind conditions in a foraging seabird

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Keywords: Accelerometer, Seabird, Behavioural adaptation, Maximum range speed, Flight behaviour, Wind.

1   ABSTRACT

2   Movement is a necessary yet energetically expensive process for motile animals. Yet how individuals

3   modify their behaviour to take advantage of environmental conditions and hence optimise energetic

4   costs during movement remains poorly understood. This is especially true for animals that move

5   through environments where they cannot easily be observed. We examined the behaviour during

6   commuting flights of black-legged kittiwakes *Rissa tridactyla* breeding on Middleton Island, Alaska in

7   relation to wind conditions they face. By simultaneously deploying GPS and accelerometer devices on

8   incubating birds we were able to quantify the timing, destination, course and speed of flights during

9   commutes to foraging patches, as well as how wing beat frequency and strength relate to flight

10   speeds. We found that kittiwakes did not preferentially fly in certain wind conditions. However, once

11   in the air they exhibited plasticity through modulation of effort by increasing air speed (the speed at

12   which they fly relative to the wind) when travelling into headwinds and decreasing their air speed

13   when flying with tailwinds. Moreover, we identified a biomechanical link behind this behaviour: that

14   to achieve these changes in flight speeds, kittiwakes altered their wing beat strength, but not wing

15   beat frequency. Using this information, we demonstrate that the cost of flying into a headwind

16   outweighs the energy saving benefit of flying with a tailwind of equivalent speed; therefore, exploiting

17   a tailwind when commuting to a foraging patch would not be beneficial if having to return in the same

18   direction with the same conditions. Our findings suggest that extrinsic factors, such as prey availability,

19   have a more influential role in determining when and where kittiwakes fly during foraging trips than

20   do wind conditions. However, once flying, kittiwakes exhibit behavioural plasticity to minimise

21   transport costs.

22

23   **Keywords:** Accelerometer, behavioural adaptation, flight behaviour, GPS, maximum range speed,

24   seabird, wind

25

26   INTRODUCTION

27   Energetic costs arising from locomotion can account for a large proportion of an animal's energy

28   expenditure (Birt-Friesen et al. 1989). Although the way in which animals move and the energetic costs

29   accrued through movement are greatly influenced by their morphology (Aerts et al. 2000, Dial 2003),

30   many species exhibit behavioural adaptations to reduce their energy costs of transport. For example,

31   great hammerhead sharks *Sphyrna mokarran* swim on their sides to exploit the greater amount of lift

32   their abnormally large dorsal fins can then generate (Payne et al. 2016), orangutans *Pongo abelii* sway

33   branches to bridge gaps in the forest canopy that they otherwise must circumvent with a route-

34   extending detour (Halsey et al. 2016, Thorpe et al. 2007) and many ungulates nod in phase with their

35   leg movements, minimising the energy required to carry their head and neck (Loscher et al. 2016).

36   Such widespread and numerous behaviours all serve to reduce the energy cost of transport,

37   suggesting that minimising this cost is beneficial (Halsey 2016).

38

39   Many seabirds forage for extended periods of time at sea, often facing the challenge of commuting

40   between patches of accessible prey. Some seabird species are exemplars of exploiting the ocean

41   environment in a way that minimises transport costs from commuting. Soaring seabirds with low wing

42   loading, such as albatrosses and frigate birds, can exploit the windscapes they encounter to travel vast

43   distances while expending very little energy (Shaffer 2011). This shapes not just the way in which they

44   fly, but also where they choose to fly (Weimerskirch et al. 2016, Weimerskirch et al. 2000,

45   Weimerskirch et al. 2012). However, at the other extreme, species such as auks and shags, which have

46   a high wing loading and need to continuously flap to stay in flight, face exceptionally high flight costs

47   (Elliott et al. 2013a, Elliott et al. 2013b) that can be exacerbated by strong winds (Elliott et al. 2014).

48   This raises the question as to whether seabirds that employ flapping flight exhibit behaviours that limit

49   the considerable energy costs their flying can entail. For example, do they adapt their flight timings

50   and destinations in response to the wind conditions they face (as has been recorded in bird species

51   during migratory flights (Åkesson and Hedenström 2000, Liechti 2006, Mateos-Rodríguez and

52   Bruderer 2012)), or, once in the air, do they adjust their flight behaviour to optimise efficiency?

53

54   During the breeding season, seabirds are central-place foragers and not only face the direct energetic

55   costs of raising young (Regular et al. 2014), but also the time and energy costs of frequently

56   commuting between their breeding site and foraging grounds. How individuals respond to

57   environmental conditions such as prevailing wind conditions during this period of high energy

58   demand, hampered by time-constrained movement (Gales and Green 1990, Shaffer 2004), is poorly

59   understood for most seabird species. This is largely due to flight being particularly difficult to study in-

60   situ (Elliott 2016, Guigueno et al. 2019). Theoretical approaches to understanding behaviour during

61   flight have led to aerodynamic models that predict how individuals might fly to minimise their

62   transport energy costs (Pennycuick 2008). Two different strategies have been proposed to explain

63   how continuously flapping birds might adjust their flight: maximum range speed and minimum power

64   speed. Maximum range speed is the air speed that covers the greatest air distance per unit of energy,

65   while minimum power speed is the air speed corresponding to the lowest required rate of energy

66   expenditure to stay in flight. Minimum power speed leads to the longest time spent flying without

67   needing to refuel, yet does not result in the greatest distance travelled before needing to refuel

68   (Pennycuick 2008). According to optimal flight theory, minimum power speed should not be affected

69   by wind speed while maximum range speed is predicted to increase when flying into headwinds

70   (Hedenström and Alerstam 1995, Hedenström et al. 2002). Changes in flight speed are achieved

71   through changes in wing beat patterns, yet how specific wing beat patterns relate to changes in flight

72   speed during flight in the wild are not well understood. The study of flight biomechanics in the wild is

73   largely in its infancy, with much of our knowledge to date being derived from wind tunnel

74   experiments. Although valuable, the artificial environment introduces limitations that may alter

75   measures of flight behaviour (Van Walsum et al. 2019). By linking changes in flight speed to the flight

76 biomechanics underpinning them, as recorded in-situ, a more complete understanding of flight

77 behaviour in the wild and its impacts on an individual's energetics can be obtained.

78

79 Biologging devices can shed light on the movement choices and flight behaviours of birds at sea (Cooke

80 et al. 2004), allowing us to investigate whether they do indeed optimise their flight in line with

81 theoretical models. To date, studies using biologging devices to examine the influence of wind on

82 seabird flight have tended to focus on the extreme soarers such as frigate birds and albatrosses (e.g.

83 (Wakefield et al. 2009, Weimerskirch et al. 2016) or, at the other end of the spectrum, species with

84 high wing loading and obligate flapping flight, such as shags (Kogure et al. 2016) and auks (Elliot et al.

85 2013a) . Less is understood about how birds with more flexible flight behaviours, which represent the

86 majority of seabirds, either utilise and/or are constrained by the wind conditions they encounter.

87 Furthermore, even less is known about how such birds might achieve changes in flight speeds through

88 nuances in flapping behaviour. In the present study we investigate the flight behaviour of the black-

89 legged kittiwake *Rissa tridactyla* (hereafter kittiwake), during the breeding season. The kittiwake is a

90 medium-sized species of gull which feeds at, or slightly-below, the sea surface. Being incapable of

91 actively pursuing prey through the water column, flight is its single mode of locomotion when

92 travelling at sea. Kittiwakes have a flap-glide style of flight, though predominate with flapping flight

93 (Birt-Friesen et al. 1989), with flight costs accounting for a large proportion of their daily energy

94 expenditure during the breeding season (Collins et al. 2016). We elucidate how breeding kittiwakes

95 respond to wind conditions during commuting flights that form part of their foraging trips, and predict

96 that this species should expend its energy stores on foraging excursions judiciously. By combining

97 simultaneous GPS and acceleration data with measures of wind speed and direction, we examine

98 kittiwake flight behaviours that operate at two spatio-temporal scales. At the broader scale we ask

99 the question: Does wind influence destination and timing of commuting flights? At a finer scale we

100 ask the question: Do kittiwakes alter their flight speeds and wing beat patterns in response to wind

101 conditions? Through linking both flight speeds and wing beat patterns, we aim to shed light on how

102   biomechanics links to bird flight behaviour and consider this in ecological terms. From our measures

103   of flight speed and wingbeat patterns, we address the question: For kittiwakes, what are the energetic

104   implications of flying against headwinds or with tailwinds?

MATERIALS AND METHODS

Data collection

We collected simultaneous GPS and tri-axial accelerometry data from 62 incubating kittiwakes

breeding on the radar tower colony on Middleton Island, Alaska (59°27'N, 146°18'W) between May

30 and June 18 2013. Accelerometers (3 g, Axy, Technosmart, Rome, Italy) were set to record at 25

Hz, while GPS loggers (14 g, CatTraQ™, Catnip Technologies, USA) were set to record at 1-minute

intervals. Both devices were attached (as a single combined unit) to the central back feathers of

kittiwakes using strips of TESA tape. Data was collected from 62 birds, however we used only those

which successfully recorded both accelerometry and GPS data simultaneously, and which recorded

data until retrieval of the loggers, thus giving a dataset of 47 combined deployments. The mean

kittiwake mass at time of deployment was 467±37 g (range 395-540 g). The GPS and accelerometer

combined weighed a total of ~ 20 g when packaged, thus accounting for a mean of 4.3% of body mass

(range 3.7-5.1%). All activities were approved by the University of Manitoba under the guidelines of

the Canadian Council on Animal Care (protocol F11-020), as well as by the US Fish & Wildlife

Service and the Alaska Department of Fish & Game. Devices of an equivalent mass have been shown

to reduce the amount of time kittiwakes spend flying, although no effects on longer term performance

measures such as reproductive success were detected in the same study (Chivers et al. 2015). The

device effect on behaviour needs to be considered when interpreting the results, however

instrumented birds still needed to (and indeed did) fly when carrying biologgers and as such we

suggest that the overall influence of wind on movement behaviour was likely to remain. A subset of

the data collected here has been analysed and interpreted in Elliott et al. 2014, however the much

larger sample size presented here (47 birds versus eight) allows us to more fully explore questions

around flight, wind and biomechanics in kittiwakes.

We used a weather dataset from the Middleton Island Airport that comprised of wind speed and wind

direction   recorded   within   1   km   of   the   colony   at   20   min   intervals

131 (http://cdo.ncdc.noaa.gov/qclcd/QCLCD). We collated these data from the start time of the first

132 logger dataset to the end of the last. To characterise the overall prevailing wind conditions and to

133 identify if there was an association between time of day and wind conditions, average wind speed and

134 direction per hour of the day were calculated and visualised using the "metvurst" package in R 3.2.1

135 (R Core Team 2014).

136

137 *Behavioural assignments*

138 To identify periods of flight and full foraging trips, acceleration data were assigned to three coarse-

139 scale behaviours: "nest attendance", "on water", and "flying". Although finer-scale behaviours such

140 as foraging, preening, and courtship are exhibited by kittiwakes, the amount of time these behaviours

141 take up is relatively little (Jodice et al. 2003). As per Collins et al. 2015, behaviours were assigned using

142 a simple method that categorises different activity types based on readily calculable metrics indicating

143 body orientation or amount of movement. Behaviours were assigned per second of accelerometry

144 data. Behaviours of "nest attendance" and "on water" were assigned depending on the body angle of

145 the bird; periods when the bird was at a lower angle were assigned as "on water", and periods at

146 which the bird was at a higher body angle were identified as being on land. The body angle thresholds

147 at which these behaviours were separated were specific to each individual. When classified as on land,

148 birds were assumed to be attending their nest, and were thus assigned the behaviour "nest

149 attendance". Flight was assigned based on the standard deviation of acceleration values in the heave

150 axis, with higher values indicating movement in this channel relating to flight. This method of

151 behavioural classification has been shown to give high accuracy (>95%) of coarse-scale behaviour

152 assignments in kittiwakes (Collins et al. 2015). However, to further enhance the accuracy of this

153 approach, a rule was applied to the data whereby assignments of "on land" could not be assigned

154 when accompanying GPS data indicated that the bird was at sea; likewise when GPS data indicated

155 that the bird was over land an assignment of "on water" could not be made. Foraging trips were

156 defined as a period in which the bird flew from the land, spent time on water, and then returned to

157   the land, with trips varying in duration. Only trips over 30 min were used, to exclude periods when

158   birds might have left the land for reasons other than foraging (such as researcher disturbance or

159   predator avoidance (Collins et al. 2014)). Flight was not separated into flapping or gliding, although

160   kittiwakes flap much more than they glide (Birt-Friesen et al. 1989), as verified by visual examination

161   of the raw heave axis acceleration data.

162

163   ***Spatial analysis***

164   As per (Warwick-Evans et al. 2015) we interpolated GPS tracks to one fix per second using the

165   "adehabitatLT" package (Calenge 2006) in R 3.2.1 (R Core Team 2014) so that it was at the same

166   frequency as, and could therefore be combined with, accelerometry behaviour data. We used the

167   "geosphere" package in R (Hijmans et al. 2012) to measure the distance between interpolated GPS

168   locations to calculate total distance travelled and maximum distance from the colony.

169

170   ***Kernel density analysis***

171   We used the Geospatial Modelling Environment software (Beyer 2012) to estimate the kernel

172   densities and the 50% kernel home ranges of the birds' at-sea distributions. Only data relating to when

173   birds were in flight (as indicated by prior behavioural assignments) were included in the distribution

174   density estimates. This analysis therefore reflects foraging destinations and flight directions, rather

175   than areas where the birds may have spent a large amount of time loafing on the water. Cell size was

176   set to 1 km^2 while the bandwidth was obtained using the plug-in estimator (Wand and Jones 1994) in

177   the "ks" package (Duong 2015) in R.

178

179   ***Flight speeds and direction***

180   GPS data were used to calculate measures of flight speed per second. The ground speed vector V_g (the

181   speed of flight measured from the GPS track) was calculated by dividing measured distance travelled

182   by time taken, while the air speed vector V_a (the speed the bird is flying after accounting for the speed

183 and direction of the wind) was measured by subtracting the wind speed vector V_w from ground speed

184 vector (Kogure et al. 2016):

185 $V_a = V_g - V_w$

186 Wind data were interpolated between each twenty minute sampling interval and matched to

187 associated GPS data point as measured per second. The wind speed vectors (which we refer to as

188 tailwind speed in our analyses) were calculated by estimating the wind vector in direction of flight

189 parallel to the bird as measured by GPS heading using the "RNCEP" package (Kemp et al. 2012) in R.

190 All speeds were calculated in m s^{-1}. Although ground and air speeds were calculated for all flights, we

191 excluded from our analyses flights relating to periods when the birds were most likely foraging -

192 identified through measures of speed estimated in R and visual inspection of the data in ArcGIS (ESRI,

193 USA, version 10.0) as having high tortuosity and low ground speeds. Foraging was omitted so that we

194 could focus on the influence of wind on commuting flights alone. Flight speeds used in analyses are

195 averages across each flight, with the first and last 50 seconds removed to reduce the influence of

196 changes in speed during take-off and landing.

197

198 Flight direction was examined at two scales. To understand the general direction of travel for first and

199 last commuting flights in a foraging trip, the direction between the first (take-off) and last (landing)

200 GPS fixes of these flights were calculated. Whereas to identify if birds preferentially flew with wind

201 assistance when in flight, the angular difference between the direction of flight and wind direction

202 during flight was calculated. Direction of flight was subtracted from wind direction per second during

203 each flight and then averaged across each full flight. By calculating this value per second we account

204 for potential changes in both wind and bird direction during flights. To identify if there was any

205 significant deviation from a uniform distribution of angular differences between flight and wind

206 directions we conducted a Rao's spacing test (alpha = 0.05).

207

208 **_Wing beat parameters_**

209   Dominant wing beat frequency was calculated using peak spectral density on Fast-Fourier transformed

210   acceleration values (g) in the heave axis (the dorso-ventrally orientated axis). It was calculated across

211   commuting flights, however the first and last 50 s of each flight was removed due to wing beat

212   frequencies being more variable during take-off and landing (Elliott et al. 2014). Wing beat strength,

213   was assumed to be directly proportional to body movement amplitude (Van Walsum et al. 2019). As

214   per Kogure et al. 2016, wing beat strength was calculated using the Ethographer application

215   (Sakamoto et al. 2009) in IGOR Pro (Wavemetrics inc., USA 2008, Version 6.37). Continuous wavelet

216   transformation was applied to the raw acceleration data in the heave axis (g), and wing beat strength

217   was calculated as the average of absolute amplitude of each waveform every second. As with

218   estimates of wing beat frequency, the values we derived relate to the dominant wing beat strength

219   across each commuting flight period, with the first and last 50 s of each flight removed.

220

221   ***Statistical analysis***

222   All inferential statistical analyses presented relate to values derived across individual flights. Only

223   flights of a duration of more than 5 min were included in the analyses to ensure that the dominant

224   wing beat frequency and dominant wing beat strength measurements were more likely to represent

225   the dominant signal rather than an outlying value from highly variable signals.

226

227   A series of generalised linear mixed models (GLMMs) were constructed to test for the influence of

228   wind on various aspects of flight behaviour. GLMMs were constructed for both flight duration and

229   total distance travelled in relation to wind speed and direction. Further GLMMs were then constructed

230   to examine the influence of the wind speed component in the direction of travel (hereafter tailwind

231   speed) on estimated air speeds, reflecting the effort of birds in the face of varying wind directions at

232   different ground speeds across flights. Following (Shamoun-Baranes et al. 2007), and as implemented

233   by (Kogure et al. 2016, Yoda et al. 2012), we also applied a two-dimensional GAM to analyse the

234   relationship between air speed and wind speed during flights. Wind speed was separated into two

235 components - headwind speed and crosswind speed - and was transformed via LOESS transformation

236 (with a maximum span of 80% and 2 degrees of freedom). Analysis was conducted in the "mgcv"

237 package (Wood 2001) in R. This additional analysis was carried out to identify if findings from the

238 GLMMs were likely to be spurious correlations that can arise from analysing wind data with a one-

239 dimensional model (Shamoun-Baranes et al. 2007). We also constructed GLMMs to identify how air

240 speed was related to the dominant wing beat frequency and wing beat strength for individual flights.

241 Due to each kittiwake undertaking numerous flights during the period in which they were measured,

242 individual bird identity was assigned as a random factor in all GLMMs. All GLMMs were constructed

243 with a Gaussian family and a log link due to each response variable conforming to assumptions of

244 normality. GLMMs were constructed using 'glmmPQL' from the MASS package (Venables and Ripley

245 2002) in R. P values below 0.05 were deemed to be statistically significant.

246

247 RESULTS

248 ***Broad-scale behaviour***

249 *Distribution and direction of flights*

250 We detected a total of 107 foraging trips, which included a total of 558 discrete flights with a duration

251 of 5 min or more. Mean foraging trip duration was 4.3±0.4 h (n=77), with mean percentage of total

252 time spent in flight throughout a foraging trip being 47.3±2.5%. The mean total distance travelled per

253 foraging trip was 73.3±5.1 km (range 10.7-201.9 km), with the mean maximum distance from the

254 colony being 21.6±1.4 km (range 3.0 – 57.6 km). On average, foraging trips included 5.2±0.5 discrete

255 flights (range 1 – 26) separated by either feeding bouts or periods of resting on the water. In total, 402

256 of these flights were classified as commuting flights, thus fitting the criteria for subsequent analysis.

257 Mean duration of these flights was 12.1±0.68 min, covering a mean distance of 5.18±0.41 km.

258

259 The majority of recorded foraging trips were to the north, or slightly northeast, of the colony (Figure

260 1). The 50% kernel density estimates for space use when on a foraging trip highlight the importance

261 of the area immediately to the North of Middleton Island (Figure 1). 94% of initial flights headed

262 northwards between 315 - 135°, whilst 87% of final flights in each foraging trip (i.e. the return trips)

263 headed southwards, between 135-270° (Figure 2). The mean angular difference between the first

264 outwards and the last return flight across all foraging trips was 167.8±4.7°.

265

266 *The influence of wind on initiation and direction of flights*

267 Throughout the study period winds tended to come from either a south to south westerly direction

268 (200-270°) or from a north-easterly to easterly direction (40-100°). Mean wind speed was 4.2±0.1 m

269 s^{-1} (range=0-11.2 m s^{-1}). There was no diurnal pattern in wind direction or wind speed (Figure 3).

270

271 Hourly wind direction weighted by the number of birds equipped during each hour, and thus indicating

272 available wind conditions for study birds to fly in, reflected the dominant wind conditions over the

273   study period, with winds blowing from either a south to westerly direction or a north east to easterly

274   direction (Figure 4a).

275

276   Birds showed no clear preference for flying during periods when the wind was blowing from certain

277   directions or at certain speeds. The distribution of wind conditions during: all flights (Figure 4b), the

278   first flight of each foraging trip (Figure 4c) and the last flight for each foraging trip (Figure 4d) did not

279   differ from the overall wind conditions during the study period (Figure 4a). Flight duration was not

280   significantly related to either wind direction (t_{357}=-0.67, p=0.503) or wind speed (t_{357}=-1.37, p=0.172),

281   however total distance travelled during a flight was significantly greater with lower overall wind speed

282   (t_{357}=-2.78, p=0.006), but was not significantly related to overall wind direction (t_{357}=-0.67, p=0.503).

283

284   There was no evidence of birds preferentially flying with tail winds when in flight. The angular

285   difference between wind direction and the overall direction the bird flew in during each flight showed

286   no significant deviation from a uniform distribution (Rao's spacing test, U=136, p>0.05). Wind speed

287   also did not appear to influence the direction the bird was travelling in relation to the wind (Figure 5).

288

289

290   ***Fine-scale behaviour***

291   *The influence of wind on flight speed and behaviour*

292   Wind speed and direction relative to the birds influenced their speed of travel. Air speed significantly

293   decreased with increasing tailwind speed (t_{378}=-18.57, p<0.001), described as: air speed=9.69-

294   0.60*tailwind speed (Figure 6a), suggesting that birds invested greater effort in headwinds and less

295   effort in tailwinds. A two-dimensional GAM identified that air speed was significantly related to one

296   or both of the wind components (tailwind and crosswind) in all individuals (P<0.001), suggesting the

297   relationship is not due to a spurious correlation.

298

299   The resultant ground speed increased significantly with tailwind speed, described as: ground

300   speed=8.38+0.34*tailwind speed (Figure 6b) (t_{382}=8.62, p<0.001) but with a lower gradient,

301   highlighting that in strong tailwinds, birds took the opportunity to reduce their flight effort.

302

303   Wing beat strength significantly increased with increasing air speed (t_{378} = 5.23, p<0.001) (Figure 7a).

304   Since air speed increases in head winds, we conclude that wing beat strength is greater in head winds.

305   There was no significant relationship between wing beat frequency and air speed (t_{378} = 1.41, p=0.160)

306   (Figure 7b). Mean wing beat frequency across all flights for all individuals was 4.07±0.01 Hz (range=

307   3.57-4.85).

308

309   DISCUSSION

310

311   By coupling positional data with body acceleration and wind data we have cast light on the interplay

312   between wind conditions, movement behaviour and the resultant potential energy implications in a

313   commuting seabird. We found that kittiwakes at Middleton Island select the location, timing and

314   course of their commuting flights apparently without consideration of the strength and direction of

315   winds they experienced, although total distance travelled was greater in lower wind speeds. For this

316   population, at least, extrinsic factors other than wind are apparently more important in determining

317   initiation and destination of their flights. Once in flight, however, kittiwakes modulate their flight

318   effort by increasing wing beat strength to increase air speed of flight in the face of headwinds. By

319   linking flight speeds to wing beat measures, we have not only provided evidence for behavioural

320   optimisation through changes in flight speeds but also identified that alteration of wing beat strength

321   is the mechanistic link underlying this behavioural adaptation.

322

323   Our finding that kittiwakes exhibited a decreased ground speed and increased air speed in response

324   to headwinds, and vice versa in tailwinds (Figure 6), builds on previous work conducted on kittiwakes

325   at Middleton Island (Elliott et al. 2014) in which a similar feature was identified on a smaller subset of

326   kittiwakes. This influence of prevailing wind conditions on flight speeds has also been recorded in

327   some other seabird species (Kogure et al. 2016, McLaren et al. 2016), supporting the idea that birds

328   adjust their flight air speed towards a 'maximum range speed'. At this air speed, the greatest air

329   distance is covered per unit of energy expended (Kogure et al. 2016, McLaren et al. 2016, Pennycuick

330   2008), as opposed to flying at a minimal power speed, whereby individuals would display the lowest

331   required rate of energy expenditure to stay in flight (i.e. being able to fly for longer rather than

332   further). This study adds to the growing body of evidence that flying towards maximum range speed

333   is a common feature of bird flight.

334

335   To achieve greater air speed when flying into stronger headwinds the kittiwakes were clearly

336   expending more energy per unit time; their increased effort manifests as an increase in wing beat

337   strength, with no variation in wing beat frequency. In accordance with our findings, adjustment of air

338   speed through moderating wing beat strength has been noted in European shags *Phalacrocorax*

339   *aristotelis* (Kogure et al. 2016). On the other hand, other species such as bar-headed geese have been

340   recorded to control flight effort and flight speeds through changing both wing beat frequency and

341   strength (Bishop et al. 2015, Schmaljohann and Liechti 2009). In Harris's Hawks *Parabuteo unicinctus,*

342   wingbeat frequency was found to be linked to climb power during ascending flights but left a lot of

343   variation unexplained, indicating that other changes in wing kinematics may be playing an important

344   role (Van Walsum et al. 2019). In Western Sandpipers *Calidris mauri* and Cockatiels *Nymphicus*

345   *hollandicus*, wingbeat frequency declined with flight speed in a wind tunnel, while lowest wingbeat

346   frequency was recorded at intermediate speed in teals *Anas crecca* and Thrush nightingales *Luscinia*

347   *luscinia* (Pennycuick et al. 1996, Hendrick et al. 2003, Maggini et al. 2017). Outside of avian flight,

348   wingbeat frequency of straw-coloured fruit bats *Eidolon helvum*, is not modified with changes in

349   speed, again suggesting other wingbeat kinematics may be more important (O'Mara et al. 2019).

350   Across a wide variety of birds and bats, flight muscle efficiency decreases with forward speed

351   (Guigueno et al. 2019), implying that any change in wingbeat frequency leads to inefficiencies in

352   conversion to mechanical work. Ultimately, the limited evidence available to date suggests that

353   different species control their flight effort through varying nuances of wing movement.

354

355   With a simple model we tested whether there is a benefit to exploiting tailwinds while undertaking

356   directed flight to and from a foraging destination. Flight costs tend to be asymmetrical, whereby the

357   costs of flying into a headwind outweigh the benefits of flying with the equivalent tailwind (Raymond

358   et al. 2010). By calculating the time required to cover a set distance of 5 km under varying wind speeds

359   using the flight speeds we calculated (ground speed [m/s] =8.38+0.34*tailwind speed [m/s]) (Figure

360   6), we can show empirically that headwinds of a certain speed are more unfavourable than an

361   equivalent tail wind speed is favourable. This appears to be the result of kittiwakes taking the

362   opportunity to substantially reduce air speed with strong tailwinds (Figure 6). The asymmetrical shape

363   of the relationship between time taken to cover 5 km and tailwind speed indicates that it takes an

364   increasing amount of time to cover a given distance as tailwinds become headwinds (Figure 8).

365   Furthermore, our analysis of wing beat patterns shows that at higher airspeeds, which tend to be

366   observed when flying into headwinds, not only will kittiwakes be flying for longer, but they will be

367   flapping with a greater wing beat strength; thus they are expending more energy both per unit time

368   and over an extended duration.

369

370   In our study, persistent wind conditions coupled with relatively short foraging trips in which individuals

371   typically return to the colony from the direction in which they headed out (average difference

372   between first outwards flight and last return flight = 167.8±4.7°; Figure 2), meant that individuals

373   waiting to exploit seemingly favourable tailwinds would not have gained an energetic advantage as

374   the return flight would have likely been into a more energetically unfavourable headwind. This could

375   well explain why we did not observe kittiwakes displaying a preference for initiating commuting flights

376   in either direction to either the strength or direction of wind conditions (Figures 4b-4d). Conversely,

377   there has been some indication that soaring seabirds such as fulmars leave their nests to forage more

378   frequently during stronger winds, when they would benefit from wind assistance (Furness and Bryant

379   1996). This contrast to the kittiwakes make sense as fulmars employ a soaring style of flight as opposed

380   to the predominantly flapping flight employed by kittiwakes. However, kittiwakes flying in lower wind

381   speeds travelled larger total distances. This could give some advantages as it would enable them to

382   move more rapidly between foraging patches (Weimerskirch et al. 2012) and hence possibly allow

383   more time to be spent foraging.

384

385   In addition to not initiating flights to exploit tailwinds, we also identified that when in flight, the

386   kittiwakes did not adjust their direction of flight in relation to the wind (Figure 5). This is in contrast to

387   species such as albatrosses and red-footed boobies, which show behavioural adjustment of flight

388   paths to ensure they minimise the proportion of time they fly into headwinds (Wakefield et al. 2009,

389   Weimerskirch et al. 2005). Possibly, the wind conditions experienced by kittiwakes at Middleton Island

390   do not typically reach sufficient strength to either blow them off course or influence their decisions

391   about where to fly. The wind conditions during the study period did not consist of prolonged periods

392   of high winds (Figures 3 and 4); average wind speed over the study period was 4.2 ± 0.1 m s^{-1}. This is

393   similar to the average wind speeds across the full breeding period, (between March and September),

394   which averaged 4.8 ± 2.8 m s^{-1}. In a study on breeding kittiwakes across two contrasting islands, wind

395   speed was a deterministic factor in initiation and location of foraging flights in one of the colonies, but

396   not the other (Christensen-Dalsgaard et al. 2018). It seems that the nuanced interplay between

397   intrinsic and extrinsic factors are likely to influence the importance of wind conditions on foraging

398   behaviour between different colonies. The wind conditions experienced by kittiwakes on Middleton

399   Island in this study were quite consistent - examining how they respond to more variable wind

400   conditions could help identify at which point wind might play a more deterministic role in influencing

401   timing and direction of commuting flights. It is also a possibility that by measuring wind conditions at

402   a coarse scale at one fixed point, we did not fully capture the diversity in wind conditions the kittiwakes

403   in our study faced when out at sea. This is unlikely to impact our findings relating to flights when

404   departing the colony, near the colony, or returning from foraging trips, however finer scale wind

405   information better matched to that gathered from the birds could allow further confidence in our

406   findings.

407

408   Not only did the kittiwakes demonstrate great consistency in flight direction but also in foraging

409   destination, the latter quite possibly explaining the former (Figures 1 & 2). This suggests they were

410   exploiting a reliable food source. As we do not have prey density data for the area surrounding the

411   study colony we cannot confirm this supposition. However, the association of foraging destination

412   with areas of high prey availability has been demonstrated in many seabird species (Burke and

413   Montevecchi 2009, Fauchald and Erikstad 2002, Raymond et al. 2010, Weimerskirch 2007). The

414   consistency of foraging destination, absence of preference for flying out to that destination during

415   favourable wind conditions, and the lack of adjustment of flight course in response to wind speed and

416   direction suggest that wind was not a deterministic extrinsic factor shaping the commuting flight

417   behaviour of kittiwakes at Middleton Island during the study period. It is likely that prey availability,

418   or perhaps time constraints requiring kittiwakes to reach prey quickly, superseded wind speed and

419   direction in determining the broader-scale features of their commuting flights.

420

421   ***Conclusion***

422   Middleton Island kittiwakes seem unperturbed by the wind conditions they experience when

423   commuting to and from foraging patches. Perhaps the additional energy costs of unfavourable winds

424   are negligible or unimportant to them, or perhaps waiting for better conditions is outweighed by the

425   time lost to not feeding at reliable foraging sites. Another possibility is that persistent winds and

426   relatively short foraging trips mean the same wind conditions will be experienced both on the outward

427   and return journeys, nullifying the value of tailwinds on one leg of the trip or the other. However, once

428   in flight the birds respond to wind conditions by adjusting the pattern of their wing beats apparently

429   to take advantage of tailwinds and minimise the impact of headwinds, thus optimising the speeds at

430   which they fly in terms of minimising the energy they expend.

431

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575

576 **Figures**

577
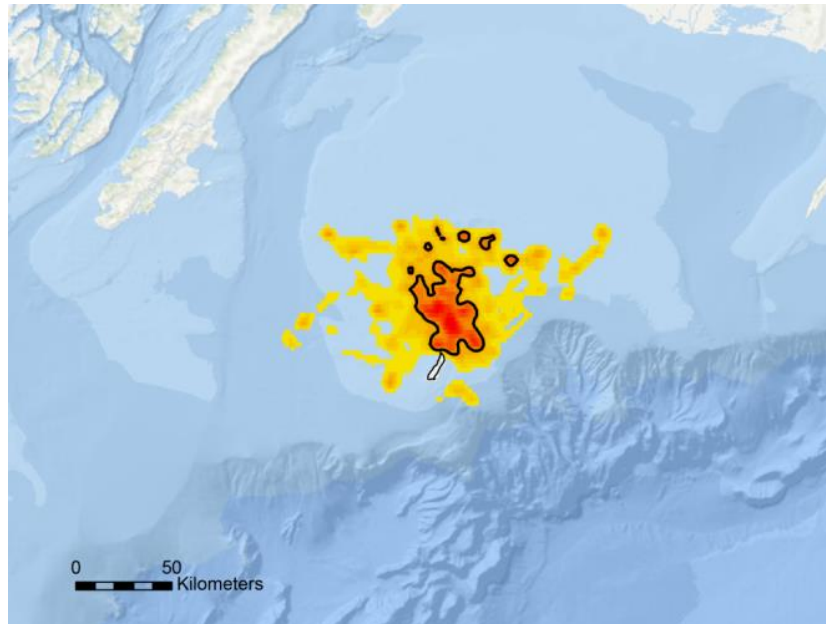
578

579 **Figure 1.** Kernel density for the distribution of all foraging trips across the study period. The intensity

580 of the yellow to red colours indicates density of GPS fixes, with the darker red indicating higher

581 density. The solid black line surrounding the red represents the 50% kernel estimates. Middleton

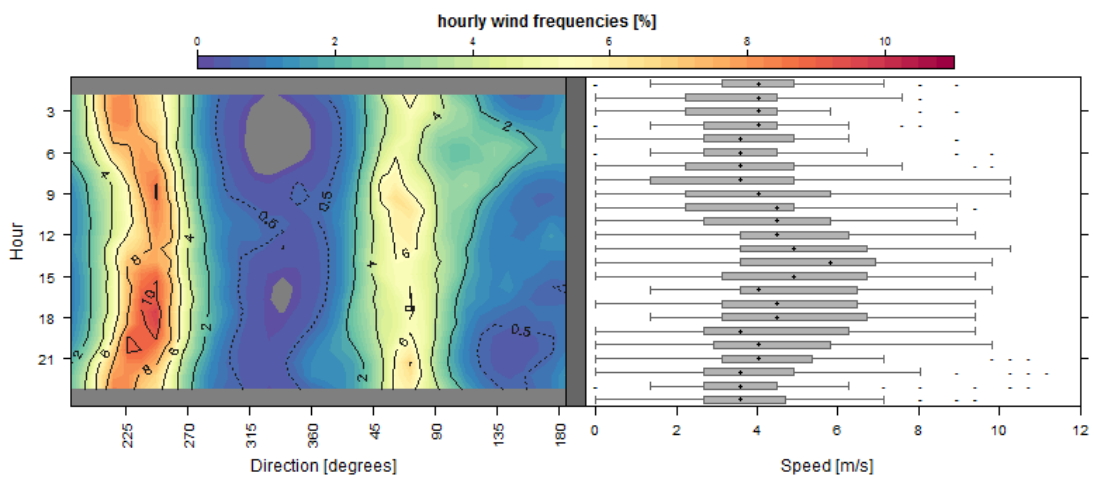582 Island is the white shape central to the image, just below the 50% kernel outline.

583
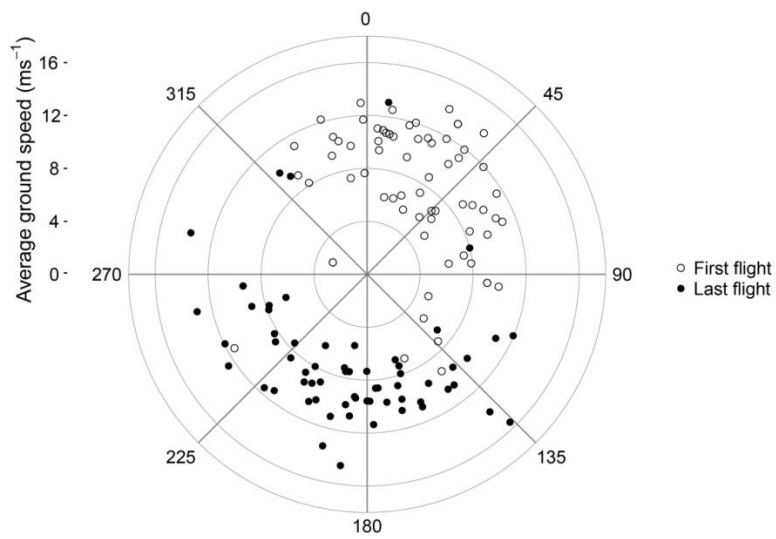
584

585 **Figure 2.** Direction flying towards, and average ground speed of, the first and last flight for each

586   foraging trip.

587

588

589 **Figure 3.** Wind contours for the full duration of the study. The left hand panel indicates hourly

590 frequencies of wind direction, while the panel on the right indicates the distribution of wind speeds

591 per hour. Note that charts indicate the direction wind is coming from.

592
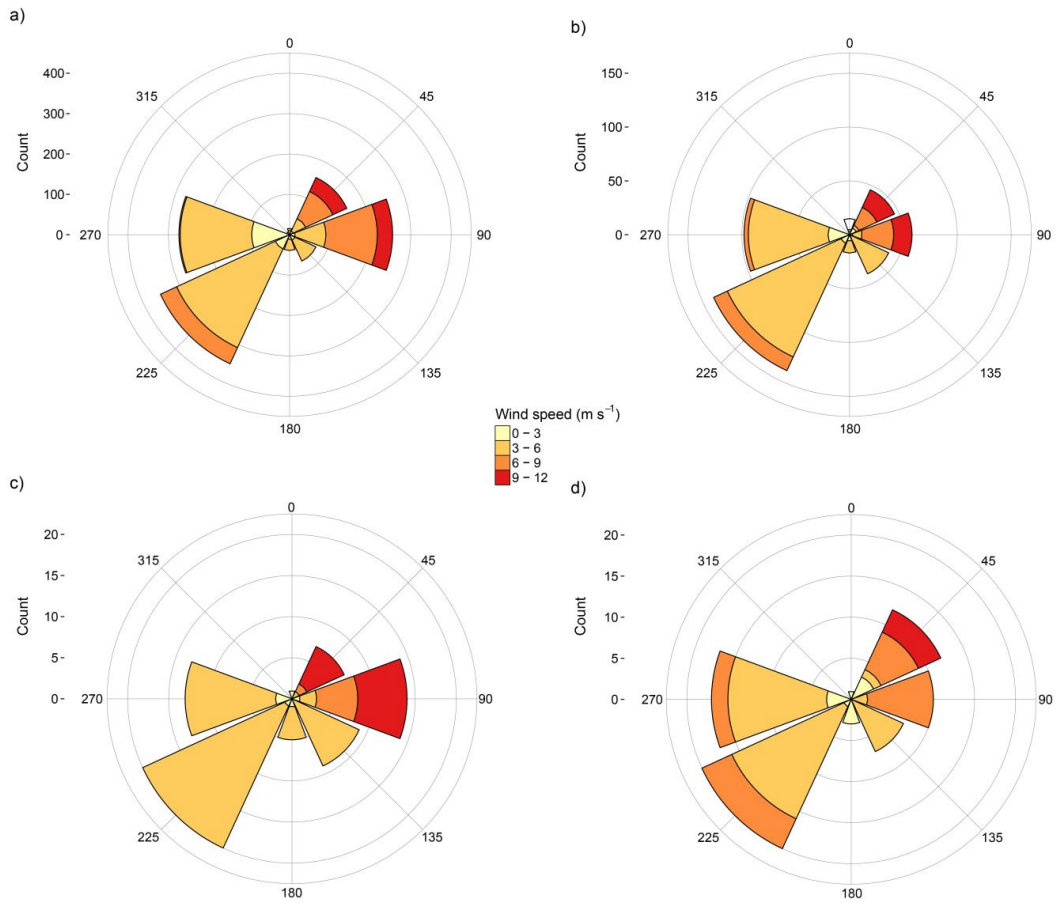
Figure 4 – Wind rose diagrams showing wind direction and strength for: a) the full study period weighted by sample size, b) all flights, c) the first flight from each foraging trip, d) the last flight from each foraging trip. Note that charts indicate the direction wind is coming from.

596
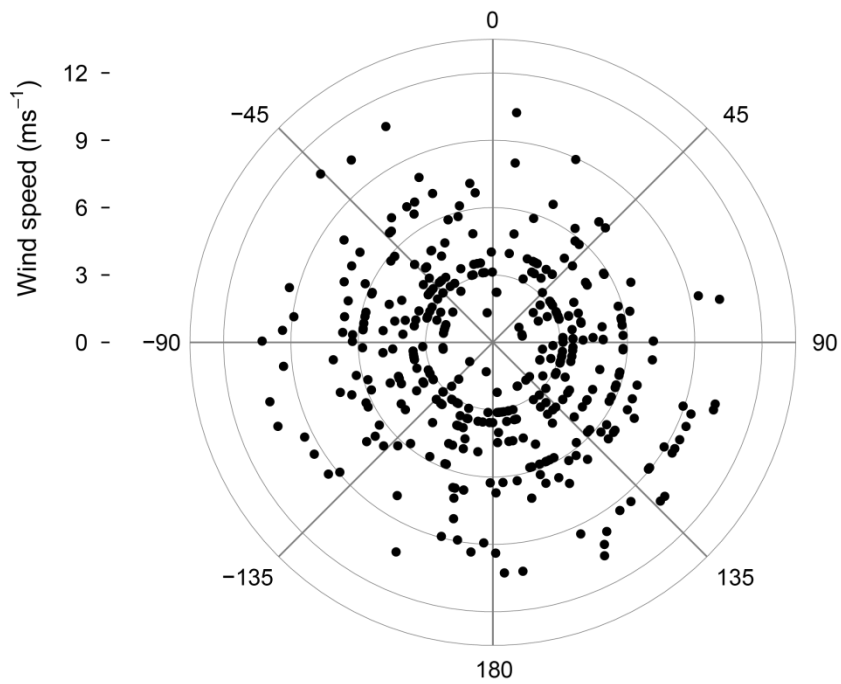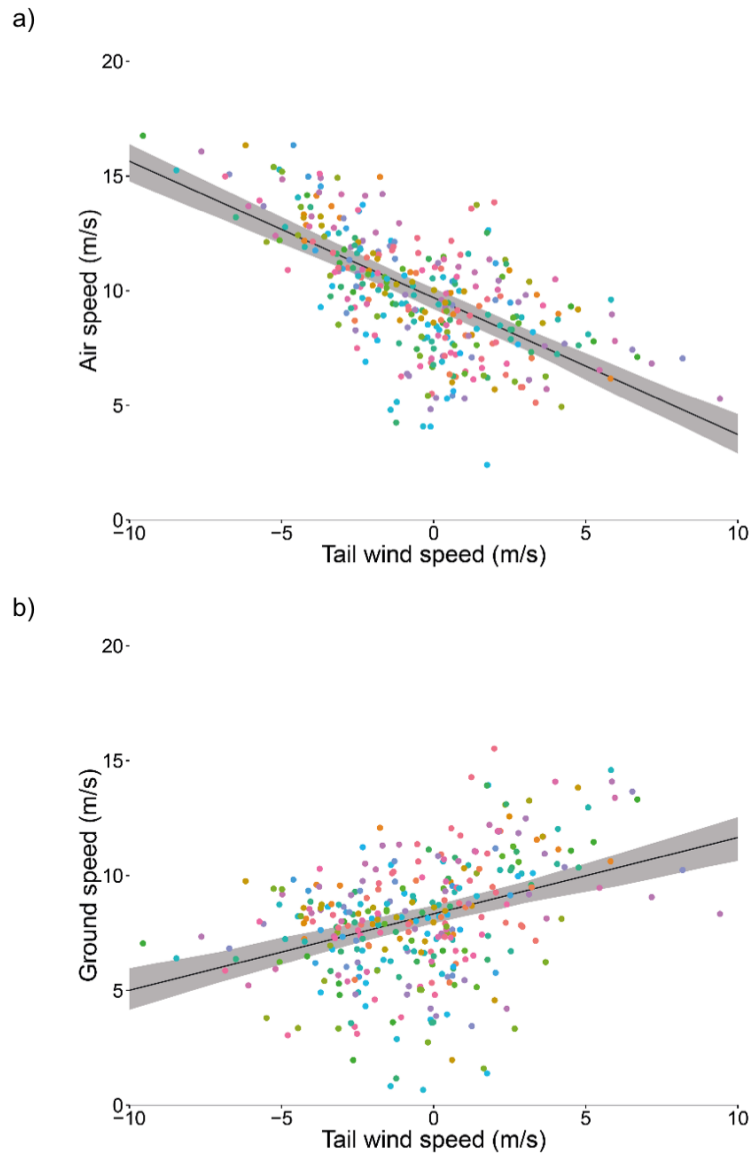
Figure 5 The angular difference between flight direction and wind direction for all flights. Each black

dot represents a flight. Values closer to 0 represent birds flying with a tailwind, whereas values of 180

indicate flights in which birds were flying with a headwind.

Figure 6 The relationship between tailwind and a) air speed; b) ground speed for all flights over 2 min. Each colour represents an individual bird. The solid line indicates the fixed effect relationship, with the grey ribbon indicating the 95% confidence intervals. Positive values along the x-axis indicate tail winds in relation to the bird, whereas negative values indicate a headwind.
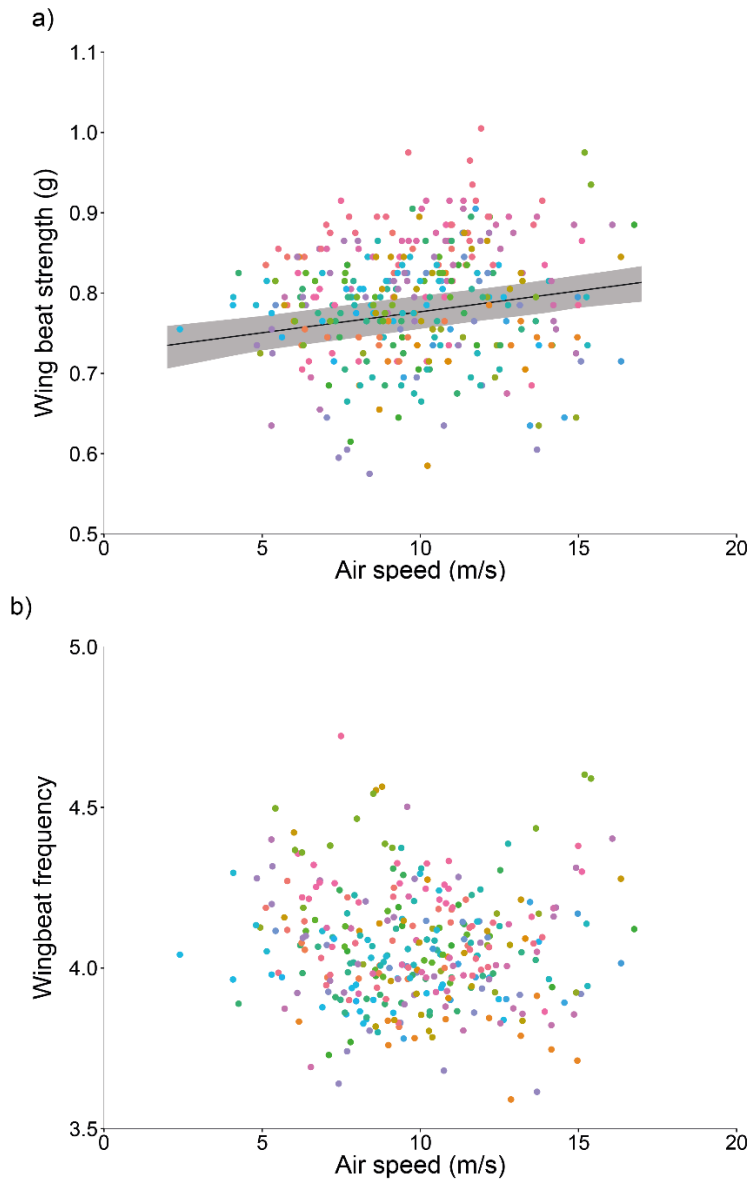
Figure 7 The relationship between air speed and a) wing beat strength and b) wing beat frequency for all commuting flights. Each colour represents an individual bird. The solid line indicates the fixed effect relationship, with the grey ribbon indicating the 95% confidence intervals.
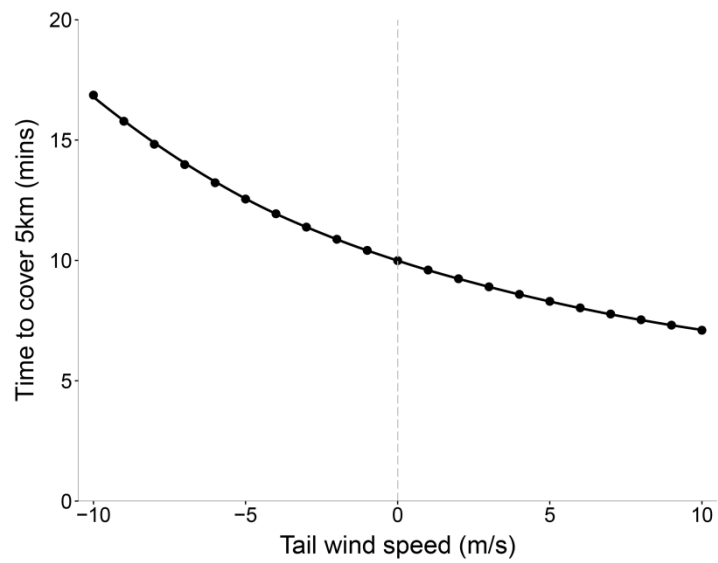
609

610 **Figure 8** The time taken for kittiwakes from Middleton Island to travel 5 km over the ground in a

611 straight line dependent on wind speed. Positive values along the x-axis indicate tail winds in relation

612 to the bird, whereas negative values indicate a headwind. Times were calculated from the

613 relationship between ground speed and tailwind described in Figure 4.6a (ground speed [m/s]

614 =8.38+0.34*tailwind speed [m/s]). The curved line is a smoothed conditional mean, calculated using

615 a LOESS estimator.

616

617

618