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Paper:

Borger, L. (in press). Impact of changing wind conditions on foraging and incubation success in male and female wandering albatrosses. *Journal of Animal Ecology*

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Impact of changing wind conditions on foraging
and incubation success in male and female
wandering albatrosses

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Word count (including title page, figures, table and references): 7947 (max
allowed 8500).

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1 Summary

1. Wind is an important climatic factor for flying animals as by affecting their locomotion, it can deeply impact their life-history characteristics.
2. In the context of globally changing wind patterns, we investigated the mechanisms underlying recently reported increase in body mass of a population of wandering albatrosses (*Diomedea exulans*) with increasing wind speed over time.
3. We built a foraging model detailing the effects of wind on movement statistics and ultimately on mass gained by the forager and mass lost by the incubating partner. We then simulated the body mass of incubating pairs and their incubation success under varying wind scenarios. We tracked the frequency at which critical mass leading to nest abandonment was reached to assess incubation success.
4. We found that wandering albatross behave as time-minimizers during incubation as mass gain was independent of any movement statistics but decreased with increasing mass at departure. Individuals forage until their energy requirements, which are determined by their body conditions, are fulfilled. This can come at the cost of their partner's condition as mass loss of the incubating partner depended on trip duration. This behaviour is consistent with strategies of long-lived species which favoured their own survival over their current reproductive attempt. In addition, wind speed increased ground speed which in turn reduced trip duration and males foraged further away than females at high ground speed.

5. Contrasted against an independent dataset, the simulation performed satisfactorily for males but less so for females under current wind conditions. The simulation predicted an increase in male body mass growth rate with increasing wind speed whereas females' rate decreased. This trend may provide an explanation for the observed increase in mass of males but not of females. Conversely, the simulation predicted very few nest abandonments, which is in line with the high breeding success of this species and is contrary to the hypothesis that wind patterns impact incubation success by altering foraging movement.

Keywords

Breeding success, energy-maximizer, environmental changes, resource allocation, resource acquisition, time-minimizer.

Introduction

1 Studies assessing ecological responses to climate change have mainly addressed the
2 effect of increasing temperature or change of rainfall regime on terrestrial species
3 (???). Less attention has been given to impact of wind changes (but see ?). For
4 illustration, in a recent review addressing the impact of climate change on bio-
5 diversity, wind was not listed among the climatic components investigated (?).
6 However winds are also responding to human-induced changes to the atmosphere
7 (?). Although the underlying mechanisms are less well understood than for tem-
8 perature and rainfall (?), winds have generally decreased over land at mid-latitude

9 in the Northern hemisphere (?) and increased over the oceans in the Southern
10 hemisphere (?).

11 Wind is a key climatic variable for flying birds (?). By impacting their locomotion and marine primary productivity (???), it potentially affects a wide range of
12 activities from foraging (??) to migration (????). In particular, wind influences
13 foraging efficiency of birds by modulating energy expenditure and movement speed
14 (?). Classical optimal foraging theory states that there is an optimal movement
15 speed during foraging (i.e. foraging speed) which maximizes energy intake rate
16 while minimizing energy expenditure rate (??). Energy intake rate can be de-
17 scribed as a function of foraging speed (???): it is expected to initially increase
18 with foraging speed by improving prey encounter rate until a threshold is reached
19 after which prey detection is negatively affected.

21 For flapping birds, energy expenditure is expected to follow a power curve
22 modulated by the wind, initially decreasing with increasing foraging speed followed
23 by an increase (??). For example, with increasing wind, murrelets and kittiwakes
24 delivered less energy to their chicks (?) probably as a result of an increasing
25 energetic cost of flight. On the other hand, northern fulmars and northern gannets
26 had higher flight costs in low wind as they had to resort to flapping flight while in
27 high wind they could rely on dynamic soaring (??), an extremely energy efficient
28 flight mode (?).

29 A specific feature of soaring flights is that their associated energy expenditure
30 is thought to be largely independent of speed as the energy required for flying is
31 extracted from the wind or air currents (???). Birds accumulate potential and
32 kinetic energy by climbing up the wind shear (?). Typically, dynamic soaring
33 flights of wandering albatrosses are composed of a series of cycles lasting about

34 10 seconds during which the bird performs an upwind climb, an upper turn, a
35 downwind descent, and a lower turn to extract energy from the wind shear as
36 wind speed increases with altitude (?). In contrast to flapping birds which have
37 to balance between energy expenditure and speed, soaring birds' ground speed
38 should be mostly determined by wind speed (?), although the observed speed of
39 albatrosses may be lower than predicted by theory (??) and the optimal speed for
40 dynamic soarers may not always be the maximum one (??).

41 The ground speed vector is the resulting vector of the wind speed vector and the
42 airspeed vector (i.e. the speed of the bird relative to the air). At very small scale,
43 ground speed is determined by the projection of the wind speed vector on the bird
44 ground speed vector (?). Yet, the direction of flight relative to the wind changes
45 with increasing spatial scale (?) and thus, the relationship between the projection
46 of the wind vector on the large-scale ground speed vector and ground speed is
47 no longer as meaningful. On average, on a large scale, wandering albatrosses can
48 appear to fly with crosswinds because they turn from upwind to downwind. Indeed,
49 at large-scale patterns, crosswind is the most frequent wind direction relative to
50 ground speed (?). Dynamic soaring also allows general direction of flight to be
51 upwind, yet in this case, large scale patterns show a meandrous trajectory (?).
52 Thus at large scale, bird ground speed is mostly expected to be determined by
53 wind speed (??).

54 Although animals constantly need to optimize their time and energy budget
55 to survive (??), this budget is under stronger constraints during reproduction.
56 Species providing pre- and postnatal parental care, like most bird species typically
57 have high energy requirements when rearing young (??) while having to acquire
58 food in a limited amount of time. Chick survival and quality depend upon the

59 amount of energy received and the time of delivery, and incubation success de-
60 pends upon the acquisition of resources and the length of the incubation shift.
61 Many long-lived seabirds only allocate a limited amount of resources to reproduc-
62 tion, favouring their own survival over a single reproductive event (???). During
63 incubation, if their body reserves are nearly exhausted before the return of their
64 partners, breeders abandon the nest to return at sea to feed (???). If insufficient
65 energy is gathered or if the forager returns too late, reproduction fails.

66 Wind can ultimately impact reproductive success by determining the amount
67 of energy gathered or the foraging trip duration of soaring birds depending on the
68 foraging strategy used. Birds behaving as time minimizers (?) during reproduc-
69 tion, i.e. having fixed energy requirement, are expected to return as soon as their
70 energy requirements are met. Thus, exposed to windy conditions, soarers can be
71 expected to forage at a high optimal speed, gather their resources in a shorter
72 amount of time and return to the nest sooner. This would imply an initial neg-
73 ative relationship between flight speed and foraging trip duration and a weak to
74 no relationship between foraging trip duration and energy intake. On the other
75 hand, energy maximizers (?), i.e. having a fixed amount of time to allocate to
76 foraging, return as soon as the time is out. At high optimal speed, achieved in
77 windy conditions, they should forage for the same amount of time but return with
78 more energy. In this case, flight speed is expected to increase food intake but not
79 foraging trip duration.

80 The wandering albatross performs dynamic soaring and can reach very high
81 speed in strong wind (?). The winds of the Southern Indian Ocean, where pop-
82 ulations of wandering albatross breed, are correlated with the Southern Annular
83 Mode (SAM). For the past two decades the SAM has shown a positive trend, in-

84 ducing stronger winds shifting towards the pole, with mean wind speed predicted
85 to reach up to 15m/s by 2080 compared to 8-9m/s today (??). This trend is fur-
86 ther enhanced by global warming (?). In this context, investigating how wandering
87 albatrosses react to long-term change to wind is needed to assess impacts on their
88 demography.

89 There is evidence that the population of Crozet Islands is undergoing body
90 mass changes in response to wind changes. Over the last 20 years, the average
91 individual has gained close to 1 kg (more than 10% of their body mass) concurrent
92 with an increase in westerly winds (?). There has also been an increased breeding
93 success over the past decades, suggesting a link between climate change, body
94 mass and reproduction (?).

95 The incubation is of particular importance for this long-lived species as most of
96 breeding failures occur during this phase due to nest abandonment (?). Breeders
97 share incubation duty equally: when one partner is foraging, the other is fasting
98 on the nest. It is during this period that a reduction in mass loss of the incubating
99 partner can have the highest impact for breeding success and consequently on
100 demography.

101 In this study, we investigated whether wind changes could cause the observed
102 overall mass gain and higher breeding success by improving foraging efficiency
103 during the incubation period. To do so, we determined the foraging strategy
104 of wandering albatrosses during incubation using relocation data. The outcome
105 of a foraging trip can be evaluated by the associated mass gain and the mass
106 lost (during the incubation shift) by the incubating partner. Both can depend on
107 movement statistics including foraging trip duration, ground speed, and maximum
108 distance from the colony, which in turn can be affected by each other and/or the

109 wind.

110 Whether wandering albatrosses behave as time minimizers or energy maximiz-
111 ers during incubation determines which, if any, movement statistics explain mass
112 gain. We tested whether absolute mass gain, a proxy for energy intake, was a func-
113 tion of trip duration, ground speed and/or mass at departure from the nest (*model*
114 *1*), and whether trip duration was reduced by ground speed and increased by the
115 most distant location reached from the colony (*model 2*). Second, we examined
116 determinants of maximum distance from the colony (*model 3*), of ground speed
117 (*model 4*) and of mass loss (*model 5*). We expected a positive effect of ground
118 speed on maximum distance (?), a positive effect of wind speed on ground speed
119 (?), and a positive effect of trip duration on mass loss (?).

120 Using the estimated parameters from these five models, we built a general
121 model detailing the effect of wind on movement statistics and ultimately on mass
122 gained by the foraging partner and mass lost by the incubating partner. We
123 hereafter refer to this model as the "foraging model". We then used this model in
124 a simulation exercise to explore the consequences of the estimated parameters and
125 relationships between variables on body mass growth rate during the incubation
126 period under different wind scenarios. From the simulation, we examined the
127 impact of wind on incubation success by tracking under which conditions and at
128 what frequency mass threshold for nest abandonment was reached.

129 **Methods**

130 **Data**

131 Two datasets were used to construct the foraging model. The first dataset was
132 collected between 2010 and 2013. 167 incubating individuals were equipped with
133 GPS tags to record their locations during foraging trips. 69 of these individuals
134 were weighed at the nest before and after their foraging trip so that their mass
135 gain is known. Complete description of the method is provided in (??). The
136 second dataset was collected between 1989 and 1991. 100 incubating individuals
137 were weighed at the nest upon arrival from and before departure for a foraging trip.
138 The duration of incubation shift was recorded but the trip of their foraging partner
139 was not tracked (see ?, for more details). Although environmental conditions may
140 have differed between the two periods and individuals of each sex were lighter
141 in the older dataset, the inclusion of mass at arrival as a covariate in the model
142 minimized the effect of this variation on mass loss rate.

143 The wind data was taken from the Blended Global Sea Surface Winds products
144 with a spatial resolution of 0.25 degrees every 6 hours from the National Climate
145 Data Center, National Oceanic and Atmospheric Administration (NOAA) website
146 (<https://data.noaa.gov/dataset/>).

147 **Foraging strategy during incubation**

148 For each of the five models, we constructed a maximal model (*sensu* ?), composed
149 of biologically plausible predictors of the response variable and performed model
150 selection to identify the predictors to include in a minimum adequate model.

151 For *model 1*, five predictors were considered to explain mass gain: mass at
152 departure (the mass difference at the nest before and after a foraging trip), trip
153 duration, ground speed (measured as the total distance covered by the bird during
154 its foraging trip while in flight divided by the time spent flying), wind speed (mea-
155 sured as the average wind speed experienced by a forager during its trip), and sex,
156 because of the strong sexual size-dimorphism of this species. Three interactions
157 were considered: sex and mass at departure, because males are on average heavier
158 than females, sex and wind speed, because males being heavier and larger have
159 a wing loading which allows them to use stronger wind than females, and wind
160 speed and mass at departure, again because of wing loading differences.

161 Although we did not expect a direct effect of wind speed on mass gain, we
162 nevertheless included it in the maximal model to look for a potential signature of
163 indirect effect of wind speed on mass gain, for example through affecting resource
164 availability. An ideal measure of body condition would have been mass relative to
165 body size, yet no reliable metric of body size was available for a significant part of
166 the individuals considered. However, as major causes of body size variation (e.g.
167 sex, stage) are included in our model, the residual variation in body mass is the
168 best measurement of body condition we currently have.

169 As wandering albatrosses are central place foragers during reproduction, trip
170 duration is likely to be affected not only by their speed but also by the most
171 distant location they reach. Trip duration (*model 2*) was expected to be explained
172 by ground speed, maximum distance from the colony (the distance between the
173 colony and the most distant point reached by the bird), their interaction, sex, wind
174 speed, and all the interactions between the continuous variables and sex.

175 Ground speed can impact the duration but also the distance covered. An addi-

176 tional model was fitted describing maximum distance from the colony by ground
177 speed, wind speed, sex and their interactions with sex (*model 3*) as birds are
178 expected to go further with stronger wind and higher speed.

179 *Model 4* examined determinants of ground speed. The predictors considered
180 were wind speed, mass at departure (to take wing loading into account), sex, and
181 the interactions between wind speed and sex, and mass at departure and sex.

182 Finally, we examined the effect of trip duration on mass loss of the incubating
183 partner (*model 5*). The predictors considered were mass at arrival to the nest,
184 duration of the partner's foraging trip, which is the same as incubation shift, sex,
185 and the interactions between mass at arrival and sex, and mass at arrival and
186 duration.

187 **Model fitting**

188 The model designed to investigate predictors of mass gain (*model 1*) used the sub-
189 set of the 2010-2013 dataset of oceanic trips for which mass gain was known (69
190 trips). The occasional continental trips were excluded because during incubation
191 these trips are usually associated with fishing boats and the mass gain was un-
192 known. Generalized least squares (GLS) were used to fit a linear regression model
193 to correct for the heteroscedasticity between the two sexes. After computing the
194 parameter of the Box-Cox power transformation which provides an empirical so-
195 lution to the optimal transformation of the response variable (?), mass gain, after
196 adding the minimum value to have exclusively positive values, was raised to the
197 power 0.55.

198 Linear mixed effect (LME) models were fitted for *models 2, 4* and *5*. A non-

199 linear mixed effect (NLME) model was fitted for *model 3* with a linear effect for
200 wind speed and an effect following the function $\frac{A}{1+\exp(N-r \cdot x)}$ for ground speed,
201 where x is ground speed and A , N , and r are the parameters to estimate. *Model*
202 *2*, *3* and *4* were fitted on the completed oceanic trips (i.e. 167 trips) from the
203 years 2010-2013. *Model 5* was fitted on the 1989-1992 dataset (127 trips, 96 in-
204 dividuals). Where necessary, response variables were transformed to satisfy the
205 assumption of normality. Individual ID was set as a random effect as some indi-
206 viduals were measured multiple times. Variables were standardized and centred
207 to allow comparison of estimates and improve convergence of the models (?).

208 Model Selection

209 Models of all possible combinations of the variables of the maximal models that
210 included sex (to account for sexual dimorphism) were ranked based on their AIC_c .
211 Only the most parsimonious model within $2 \Delta AIC_c$ of the model with the lowest
212 AIC_c was retained (?). The variables contained within this model are supported by
213 the data, as quantified by the ΔAIC_c statistics, as having an effect on the response
214 variable (?). We then calculated regression coefficients and standard errors from
215 models including these predictors to incorporate in the foraging model. We did
216 not use averaged estimates in the foraging model because the remaining predictors
217 needed to account also for the effect of the excluded predictors, which would have
218 otherwise increased the error term.

219 Goodness-of-fit of models from all LME models can be assessed by marginal
220 and conditional R^2 as described by ?. Marginal R^2 represents the proportion of
221 variance explained by the fixed effects while the conditional R^2 the proportion of

222 variance explained by both the fixed and the random effects. Pseudo- R^2 has been
223 used as an alternative measure of goodness of fit for the GLS model (?).

224 **Simulations**

225 As the response variables of one model were the explanatory variables of the next,
226 we were able to construct the foraging model from the outcome of the five ini-
227 tial models (summarized in the scheme in fig. 1). The foraging model was used to
228 simulate changes to body mass over the incubation period for 1000 wandering alba-
229 tross pairs each exposed to 12 different wind scenarios. We could use the estimates
230 from the selected GLM, LME and NLME models described in the previous section
231 to predict their values because all variables, except wind speed, are endogenous
232 to the model. To account for uncertainty, the regression coefficients were drawn
233 from a multivariate normal distribution of mean equal to the coefficient estimates
234 of the selected model and of variance equal to the variance co-variance matrix
235 between the estimates from the model. This account for the fact that there is an
236 error around the coefficient estimates and this error is not independent from other
237 estimates of the model.

238 In one scenario, wind speed was drawn for each foraging trip from a normal
239 distribution using the observed mean (8.60 m/s) with the observed standard de-
240 viation (1.38 m/s). In the other 11 cases, wind values were set for the entire
241 simulation to a value from 5 m/s to 15 m/s with an increment of 1 m/s. The
242 upper limit of wind speed was set to 15 m/s as it is the highest predicted wind
243 speed for the area by 2080 (??) and the lower limit to 5 m/s as it is unlikely
244 that wandering albatrosses can perform dynamic soaring below this threshold (?).

245 which would cause the relationship with wind to change substantially.

246 The observed average length of the incubation period is 78 days (Tickell 2000).
247 To account for this, simulations continued only if the cumulative sum of foraging
248 trips duration of a pair was below 74 days (i.e. if 73 or less days have elapsed
249 from the beginning of the incubation period when one partner returns, the fasting
250 partner leaves for one last foraging trip. If 74 or more days have elapsed when one
251 partner returns, then the simulation stops). This resulted in an average simulated
252 incubation period of 78 days under observed wind conditions.

253 Individuals started at a mass drawn from a normal distribution with mean
254 and standard deviation equal to the population mean and standard deviation at
255 the beginning of incubation for each sex. At the end of each foraging trip, the
256 mass gain was added to the mass of the forager and the mass loss subtracted
257 from the mass of the fasting partner. The critical mass below which wandering
258 albatrosses abandon the nest was calculated from the allometric equation from (?):

259

$$\frac{M}{M_t} = -0.2467 \cdot \log_{10}(M^2) + 1.7104 \cdot \log_{10}(M) - 1.3816 \quad (1)$$

260 where M is the initial mass and M_t the mass threshold. The frequency and
261 wind conditions leading to this threshold were recorded.

262 To assess whether the simulated individuals were losing or gaining mass over
263 the course of incubation, a linear regression of mass over time for each wind speed
264 value and each individual was fitted. The estimates of the fit of mass over time
265 (here after referred to as the body mass growth rate) were recorded and used to
266 fit a linear regression of the body mass growth rate over wind speed.

267 **Comparing simulation to real data**

268 To assess the reliability of body mass growth rates from the simulation, the esti-
269 mates were compared to body mass growth rates estimated from mass measure-
270 ments of 50 individuals that were weighted at least four times during incubation
271 in 1989. No individuals were tracked for the entire period. The estimates of the
272 body mass growth rates were obtained from a LME model regressing mass on time
273 with individuals as a random effect.

274 **Results**

275 **Foraging model**

276 We found that mass gain decreased with mass at departure and was higher for
277 males (*model 1*, table 1). Neither ground speed, trip duration nor wind speed were
278 included in the most parsimonious model within $2 \Delta AIC_c$ (relative importance of
279 variables: 0.33, 0.28 and 0.43, full-model averaged coefficient: -0.519 , $se=1.183$,
280 -0.299 , $se=0.931$ and 0.574 , $se=1.312$ respectively). Ground speed reduced trip
281 duration while maximum distance from the colony increased it with a multiplica-
282 tive effect (*model 2*, table 1). Maximum distance increased with ground speed,
283 especially for males although their rate of increase was lower (*model 3*, table 1).
284 Ground speed increased with wind speed (*model 4*). Mass loss increased with trip
285 duration of partner and mass at arrival to the nest as well as with their interaction
286 (*model 5*).

287 **Simulations**

288 The mass growth rates calculated from field observations showed no change in
289 mass over the incubation period (LME model: intercept (i.e. females)=7983.13 g,
290 se= 121.51, additional effect for males= 2153.99 g, se= 192.37, time effect=1.27
291 g/day, se= 3.95, additional time effect for males= -2.18 g/day, se=6.42). The
292 simulation with mean value set as the mean observed wind speed predicted pos-
293 itive mass growth rates for both sexes with a lower rate for males (LME, fixed
294 effects: intercept (i.e. females)=8396.18 g, se= 13.98, additional effect for males=
295 1736.30 g, se= 19.77, time effect=9.57 g/day, se= 0.23, additional time effect for
296 males=-7.31 g/day, se= 0.32). The mass threshold for nest abandonment was
297 never reached.

298 Exposed to average wind speed, simulated pairs performed on average 10.54 for-
299 aging trips (sd=0.50). Foraging trips lasted on average 8.24 days (sd=0.30), which
300 is shorter by 2.0 days than the observed values, (mean=10.27 days, sd= 4.81, t.test:
301 t(166)=5.55, p-value< 0.001). We found no difference between simulated ground
302 speed and the observed value (mean=11.04 m/s, sd= 1.72, t.test: t(86)=0.66,
303 p-value= 0.507). Simulated maximum distance (median=918.7 km) was lower
304 than the observed values (median=1079 km, Mann-Whitney test: W=945265, p-
305 value< 0.01).

306 Wind values were fixed in 11 simulations to range from 5 m/s to 15 m/s. The
307 simulations predicted an increase in body mass growth rate of males with wind
308 speed (linear regression: intercept= -5.81 g/day, se= 0.43, wind speed effect=1.04
309 g/day per m/s, se= 0.04) and a decrease for females (linear regression: intercept=
310 14.41 g/day, se= 0.35, wind speed effect=-0.62 g/day per m/s, se= 0.03) (see

311 fig. 2). Only two females and one male out of 12000 simulations reached mass
312 threshold for nest abandonment at a wind speed of 15 m/s.

313 Discussion

314 This study is the first (1) to propose a comprehensive quantitative estimation of
315 the links between wind speed, foraging movements and mass during incubation
316 in a species performing dynamic soaring, and (2) to explore the consequences
317 of these relationships on nest abandonment triggered by low body mass under
318 different wind scenarios. Besides confirming the effect of wind speed on ground
319 speed (???), of maximum distance from the colony on trip duration (?) and of trip
320 duration on mass loss (?), our study revealed that mass gain was independent of
321 movement statistics and also highlighted that males moved further at high speed
322 than females. Thus the simulated changes in body mass growth rates with wind
323 speed were due to a change in mass loss, which increased for females as their
324 partner foraged for longer and decreased for males as their partner performed
325 shorter trips. The simulation provided partial support for the hypothesis that
326 wind caused the mass increase reported by ? as the body mass growth rate of
327 males, but not of females, increased with wind speed. In addition, as virtually
328 no breeder's mass fell below the threshold for nest abandonment, our simulation
329 did not provide any indication that the improved breeding success reported by ?
330 was due to wind speed's indirect effect on body mass through foraging movements
331 during incubation. Yet there were some differences between the outcomes of the
332 simulation exercise and observations, calling for cautious interpretation of these
333 results.

334 The mass gain decrease with mass at departure likely reflects adjustment of
335 energy intake to body condition. This supports the hypothesis that energy is
336 the main constraint rather than time: such strong effect of body condition on
337 energy intake would not be expected if foragers were primarily time constrained.
338 This echoes the behaviour during incubation of another Procellariform, the black-
339 browed albatross (*Thalassarche melanophris*), which during a foraging trip aims at
340 regaining the mass lost during the preceding incubation shift (?). Conversely, the
341 absence of relationship between mass and ground speed and mass and trip dura-
342 tion, and the decrease in trip duration with increasing ground speed suggest that
343 wandering albatrosses behave as time-minimizers: they forage until their energetic
344 requirement are fulfilled. This self-preserving strategy, which is consistent with
345 the life-history strategy expected of long-lived species (??), could be detrimental
346 to the incubating partner if trips become excessively long. Yet, it is unlikely to
347 jeopardize reproduction as individuals have been reported to wait for their part-
348 ners for more than 40 days, far above the average trip duration (?). Excessively
349 long foraging trips may not impact breeding success immediately but later during
350 incubation or brooding.

351 Sex-specific differences in foraging behaviour are expected in species with sex-
352 ual dimorphism. For example, stronger winds caused female European shags (*Pha-
353 lacrocorax aristotelis*), flap-gliding seabirds, to forage for longer, indicating a degra-
354 dation of their foraging performance (?). The wandering albatross is no exception
355 as we found that, at high speed, males foraged further than females, but not at
356 low speed. The two sexes have distinct distributions at sea: females forage mostly
357 in areas north of the colony, whereas males tend to travel south towards the pole,
358 where they are more likely to encounter strong wind (??). The markedly different

359 climatic and oceanic conditions experienced by males and females, in combination
360 with sexual size dimorphism, could trigger the behavioural difference.

361 This distinction was incorporated into the foraging model, which describes
362 the pathway through which wind impacts mass loss of the incubating partner by
363 affecting the movement statistics of the foraging partner. At high ground speed,
364 males reached particularly distant locations, thus foraging for longer. This caused
365 their incubating partner to lose more mass whereas foraging females, performing
366 shorter trips, caused their partner to lose comparatively less mass. In strong
367 winds above 12 m/s in the simulation, males gained more mass than females.
368 Being heavy for the same body size is advantageous in strong winds (?) thus,
369 males, which fly more towards the pole where winds have increased more, would
370 be further advantaged by a higher mass gain.

371 The body mass growth rate of females predicted by the simulation did not
372 corroborate well with the body mass growth rate from *in situ* mass measurements,
373 whereas the difference was not substantial for males. Yet, the mass measurements
374 may not be representative of mass variation during incubation as no individuals
375 were tracked for the entire incubation period. Under current wind conditions, the
376 simulation predicted smaller maximum distance from the colony and shorter trips
377 compared to observation, and thus they are potentially underestimating mass loss.
378 This suggests that the predictions from the simulation should be considered with
379 caution, albeit less so for males, and need to be contrasted to future studies as
380 an overestimation of body mass growth rate can lead to an underestimation of
381 frequency of nest abandonment.

382 Yet, the very low occurrence of nest abandonment predicted by the simulations
383 may not be due only to an overestimation of body mass growth rates. Indeed,

384 individuals have been observed to abandon the nest after incubation shifts far
385 above average and others to leave after a few days even though they showed no sign
386 of resource exhaustion (?). Conditions leading to nest abandonment may not have
387 been captured by the model because they depend upon individual characteristics
388 such as inexperience, senescence or hormonal changes (?), or trip-specific events
389 such as, in extreme cases, disappearance of the forager (?). For example, breeding
390 success follows a quadratic relationship with age: young inexperienced parents
391 and old parents have a lower breeding success (??). Future research assessing how
392 age affects the relationship between wind and foraging performance may reveal
393 age-specific effects of wind on breeding success.

394 In addition, the absence of overall change in body mass from field observations
395 suggests nonetheless that the costs of incubation for wandering albatrosses are at
396 most moderate. The reproduction costs are highest during brooding (?) which is
397 reported to be 10% more expensive in terms of energy than incubation (?) and
398 the period during which breeders experience substantial mass loss (?). Yet body
399 mass of the parents at the end of incubation may impact brooding success or chick
400 quality.

401 Wind might affect breeding success through alternative mechanisms than those
402 explored here. For instance, wind may enable albatrosses to access different forag-
403 ing areas (?) and as not all circumpolar zones and fronts are equally productive
404 (?), which ones can be reached can affect foraging success. Furthermore, wind
405 can impact oceanic productivity. Indeed, high wind speed is associated with low
406 phytoplankton biomass (??) and wind interacts with eddies causing planktonic
407 bloom (?). Admittedly, wandering albatrosses forage on higher trophic levels than
408 plankton (?), yet chlorophyll *a* is frequently used as a proxy for their food avail-

409 ability (?). However, we found no direct effect of wind speed on mass gain which
410 could have hinted at a potential effect of wind on resources.

411 Our study explored how environmental change can alter the energy landscape
412 (*sensu* ?) experienced by breeding pairs of a monogamous species and how it
413 can impact the body mass of both partners. Our results did not support an
414 improved breeding success with wind through the mechanisms presented here,
415 thus highlighting the need to investigate alternative pathways to complete our
416 understanding of the effects of wind on breeding success in the wandering albatross.
417 Carry-over effects from previous life-history stages and post-incubation effects of
418 winds on reproductive success should be assessed. Nevertheless, we have shown
419 that wandering albatrosses act as time-minimizers and not energy minimizers and
420 presented a pathway through which wind can indirectly impact individual body
421 mass of a seabird performing dynamic soaring.

422 **Acknowledgements**

423 We would like to thank all the field workers involved in the field studies on Crozet,
424 S Patrick for her help with the foraging data base, and K Delord and D Besson
425 for managing the data base. We are grateful to two anonymous reviewers for
426 their helpful comments. The study was supported by the Swiss National Science
427 Foundation (SNF, grant #31003A_146445) and by the Institut Polaire Français
428 Paul Emile Victor (IPEV Program No. 109).

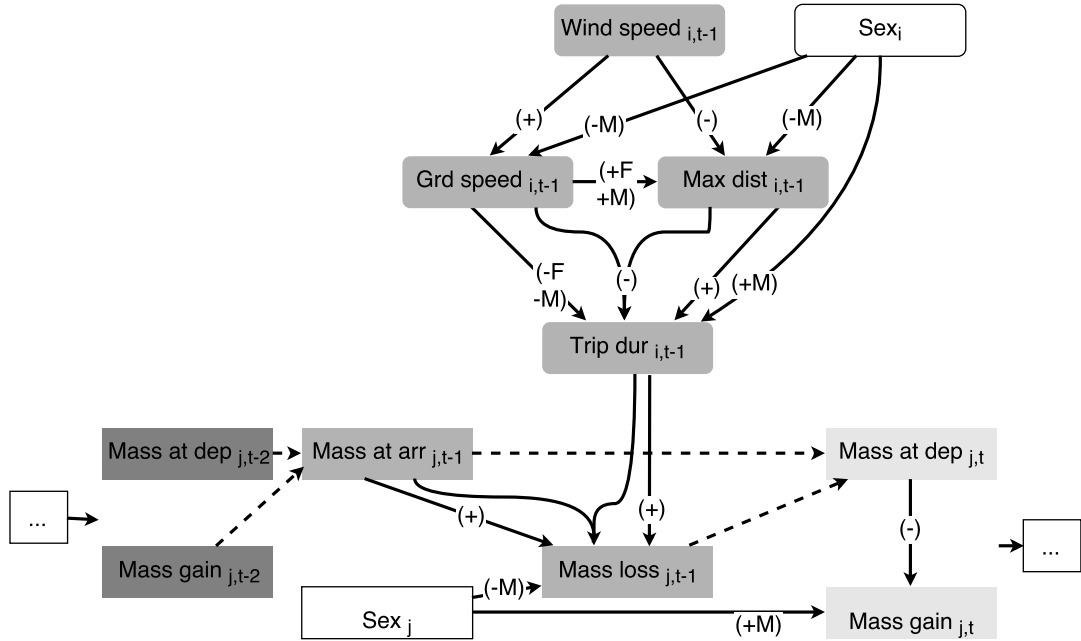


Figure 1: Scheme depicting the relationships between wind speed, movement statistics and mass of the two partners during incubation over multiple foraging trips. The shades of grey and the subscript t represent a foraging trip (from dark to light) and the shape distinguishes between the two partners (rounded is individual i , squared is individual j). During foraging trip $t - 1$, individual i is foraging and individual j is incubating. Full lines are relationships from models and the direction of the effect is indicated in the brackets, with a distinction between males (M) and females (F) when the relationship was sex-specific. Arrows at the end of a single line indicates additive effects whereas two lines joining in one arrow indicate an interaction between two continuous variables. Dashed lines represent additions and subtractions of masses from one foraging trip to the next.

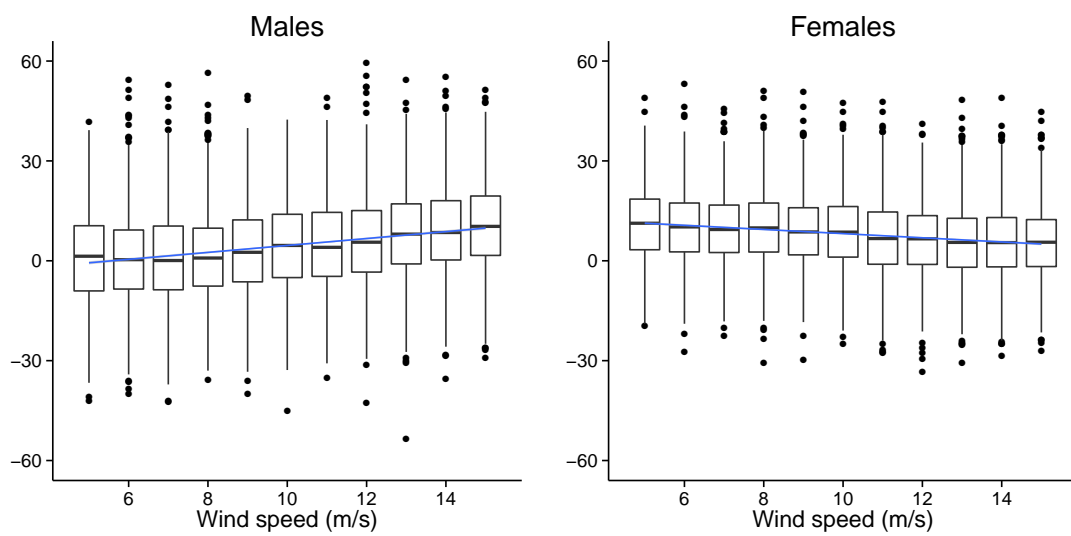


Figure 2: Body mass growth rate from the simulated mass of male and female wandering albatrosses as a function of wind speed.

Table 1: Summary of the outcome of the selection of the five models exploring the relationships between wind, movement statistics and mass. Resp. var. is the abbreviation for response variable, exp. var. for explanatory variables, se for standard error, rel. imp. of var. for relative importance of variables. Dep. stands for departure, mod for model, dur. for duration, grd for ground, max. dist. for maximum distance, marg. for marginal, cond. for conditional, arr. for arrival.

	Resp. var.	Selected exp. var.	Estimate	Se	Rel. imp. of var.
Model 1	Mass gain ^{0.55}	Intercept (female)	60.233	2.350	
		Sex (male)	13.762	5.177	fixed
		Mass at dep.	-12.338	2.437	1.00
Mod. rank: 1, Δ AIC to best mod.: 0, Pseudo-R ² : 0.44					
Model 2	log Trip dur.	Intercept (female)	2.258	0.037	
		Sex (male)	0.039	0.058	fixed
		Grd speed	-0.346	0.048	1.00
		Max. dist.	0.471	0.039	1.00
		Grd speed:max. dist.	-0.100	0.027	0.99
		Grd speed:Sex (male)	0.157	0.057	0.91
Mod. rank: 2, Δ AIC to best mod.: 0.4, Marg. R ² : 0.52, Cond. R ² : 0.58					
Model 3	log Max. dist.	A (female)	7.278	0.166	
		A (male)	1.235	0.582	1.00
		N (female)	-3.343	0.702	
		N (male)	1.941	0.791	1.00
		r (female)	1.039	0.350	
		r (male)	-0.558	0.372	1.00
Function: $\frac{A}{1+\exp(N-r \cdot x)}$, where x is grd speed					
Mod. rank: 2, Δ AIC to best mod.: 1.80					
Model 4	log Grd speed	Intercept (female)	2.398	0.021	
		Sex (male)	-0.020	0.033	fixed
		Wind speed	0.064	0.017	1.00
Mod. rank: 3, Δ AIC to best mod.: 1.18, Marg. R ² : 0.15, Cond. R ² : 0.15					
Test 5	Mass loss ^{0.5}	Intercept (female)	29.571	0.620	
		Sex (male)	-1.44	1.282	fixed
		Trip dur.	6.699	0.342	1.00
		Mass at arr.	3.060	0.638	1.00
		Trip dur.:mass at arr.	1.004	0.366	0.94
Mod. rank: 2, Δ AIC to best mod.: 1.35, Marg. R ² : 0.83, Cond. R ² : 0.83					