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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*

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

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

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

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

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

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

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

Although animals constantly need to optimize their time and energy budget to survive (??), this budget is under stronger constraints during reproduction. Species providing pre- and postnatal parental care, like most bird species typically have high energy requirements when rearing young (??) while having to acquire food in a limited amount of time. Chick survival and quality depend upon the amount of energy received and the time of delivery, and incubation success depends upon the acquisition of resources and the length of the incubation shift. Many long-lived seabirds only allocate a limited amount of resources to reproduction, favouring their own survival over a single reproductive event (???). During incubation, if their body reserves are nearly exhausted before the return of their partners, breeders abandon the nest to return at sea to feed (???). If insufficient energy is gathered or if the forager returns too late, reproduction fails.

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

The wandering albatross performs dynamic soaring and can reach very high speed in strong wind (?). The winds of the Southern Indian Ocean, where populations of wandering albatross breed, are correlated with the Southern Annular Mode (SAM). For the past two decades the SAM has shown a positive trend, inducing stronger winds shifting towards the pole, with mean wind speed predicted to reach up to 15m/s by 2080 compared to 8-9m/s today (??). This trend is further enhanced by global warming (?). In this context, investigating how wandering albatrosses react to long-term change to wind is needed to assess impacts on their demography.

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

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

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

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

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

Methods

Data

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

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

Foraging strategy during incubation

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

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

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

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

Ground speed can impact the duration but also the distance covered. An additional model was fitted describing maximum distance from the colony by ground speed, wind speed, sex and their interactions with sex (*model 3*) as birds are expected to go further with stronger wind and higher speed.

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

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

Model fitting

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

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

Model Selection

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

Goodness-of-fit of models from all LME models can be assessed by marginal and conditional R^2 as described by **?**. Marginal R^2 represents the proportion of variance explained by the fixed effects while the conditional R^2 the proportion of variance explained by both the fixed and the random effects. Pseudo-R^2 has been used as an alternative measure of goodness of fit for the GLS model (**?**).

Simulations

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

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

which would cause the relationship with wind to change substantially.

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

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

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

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

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

Comparing simulation to real data

To assess the reliability of body mass growth rates from the simulation, the estimates were compared to body mass growth rates estimated from mass measurements of 50 individuals that were weighted at least four times during incubation in 1989. No individuals were tracked for the entire period. The estimates of the body mass growth rates were obtained from a LME model regressing mass on time with individuals as a random effect.

Results

Foraging model

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

Simulations

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

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

Wind values were fixed in 11 simulations to range from 5 m/s to 15 m/s. The simulations predicted an increase in body mass growth rate of males with wind speed (linear regression: intercept= -5.81 g/day, se= 0.43, wind speed effect=1.04 g/day per m/s, se= 0.04) and a decrease for females (linear regression: intercept= 14.41 g/day, se= 0.35, wind speed effect=-0.62 g/day per m/s, se= 0.03) (see fig. 2). Only two females and one male out of 12000 simulations reached mass threshold for nest abandonment at a wind speed of 15 m/s.

Discussion

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

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

Sex-specific differences in foraging behaviour are expected in species with sexual dimorphism. For example, stronger winds caused female European shags (*Phalacrocorax aristotelis*), flap-gliding seabirds, to forage for longer, indicating a degradation of their foraging performance (**?**). The wandering albatross is no exception as we found that, at high speed, males foraged further than females, but not at low speed. The two sexes have distinct distributions at sea: females forage mostly in areas north of the colony, whereas males tend to travel south towards the pole, where they are more likely to encounter strong wind (**??**). The markedly different climatic and oceanic conditions experienced by males and females, in combination with sexual size dimorphism, could trigger the behavioural difference.

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

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

Yet, the very low occurrence of nest abandonment predicted by the simulations may not be due only to an overestimation of body mass growth rates. Indeed, individuals have been observed to abandon the nest after incubation shifts far above average and others to leave after a few days even though they showed no sign of resource exhaustion (?). Conditions leading to nest abandonment may not have been captured by the model because they depend upon individual characteristics such as inexperience, senescence or hormonal changes (?), or trip-specific events such as, in extreme cases, disappearance of the forager (?). For example, breeding success follows a quadratic relationship with age: young inexperienced parents and old parents have a lower breeding success (??). Future research assessing how age affects the relationship between wind and foraging performance may reveal age-specific effects of wind on breeding success.

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

Wind might affect breeding success through alternative mechanisms than those explored here. For instance, wind may enable albatrosses to access different foraging areas (?) and as not all circumpolar zones and fronts are equally productive (?), which ones can be reached can affect foraging success. Furthermore, wind can impact oceanic productivity. Indeed, high wind speed is associated with low phytoplankton biomass (??) and wind interacts with eddies causing planktonic bloom (?). Admittedly, wandering albatrosses forage on higher trophic levels than plankton (?), yet chlorophyll *a* is frequently used as a proxy for their food availability (?). However, we found no direct effect of wind speed on mass gain which could have hinted at a potential effect of wind on resources.

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

Acknowledgements

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

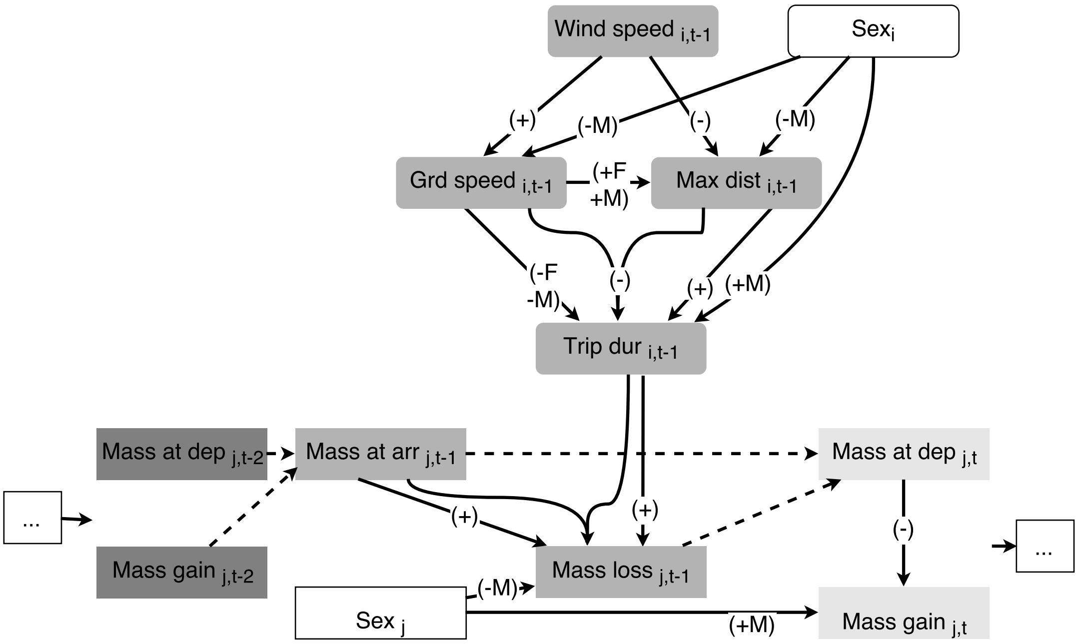

Figure 1: Scheme depicting the relationships between wind speed, movement statistics and mass of the two partners during incubation over multiple foraging trips. The shades of grey and the subscript t represent a foraging trip (from dark to light) and the shape distinguishes between the two partners (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.

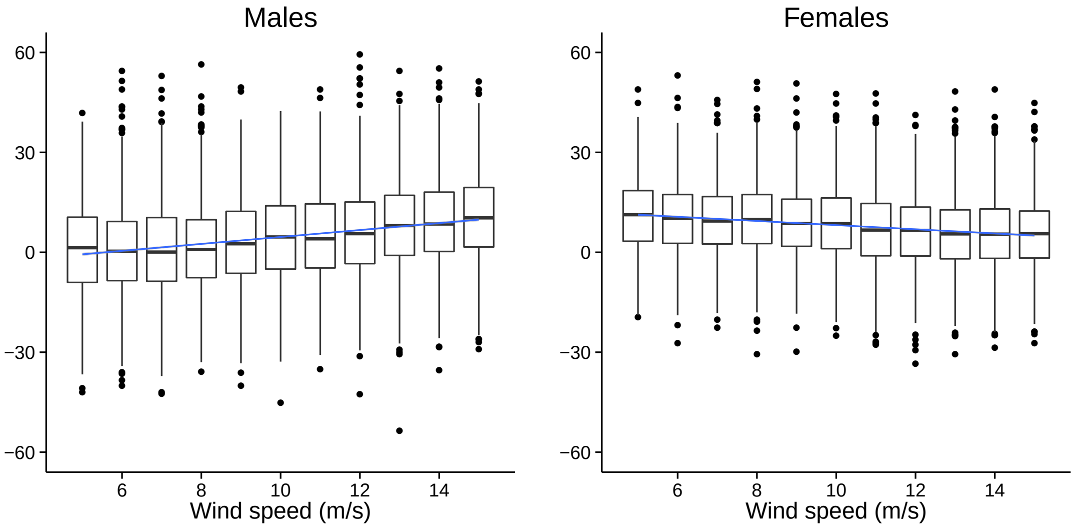

Figure 2: Body mass growth rate from the simulated mass of male and female wandering albatrosses as a function of wind speed.

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, ΔAIC 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, ΔAIC 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, ΔAIC 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, ΔAIC 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, ΔAIC to best mod.: 1.35, Marg. R^2: 0.83, Cond. R^2: 0.83					