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RESEARCH ARTICLE

Windscape and tortuosity shape the flight costs of northern gannets

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ABSTRACT

When animals move across a landscape, they alternate between active searching phases in areas with high prey density and commuting phases towards and in-between profitable feeding patches. Such active searching movements are more sinuous than travelling movements, and supposedly more costly in energy. Here we provide an empirical validation of this long-lasting assumption. To this end, we evaluated simultaneously energy expenditure and trajectory in northern gannets (*Morus bassanus*) using GPS loggers, dive recorders and three-dimensional accelerometers. Three behavioural states were determined from GPS data: foraging, when birds actively searched for prey (high tortuosity, medium speed); travelling, when birds were commuting (straight trajectory, high speed); and resting (straight trajectory, low speed). Overall dynamic body acceleration, calculated from acceleration data, was used as a proxy for energy expenditure during flight. The impact of windscape characteristics (wind force and direction) upon flight costs was also tested. Energy expenditure of northern gannets was higher during sinuous foraging flight than during more rectilinear travelling flight, demonstrating that turns are indeed costly. Yet wind force and direction also strongly shaped flight energy expenditure; within any behavioural state it was less costly to fly with the wind than against it, and less costly to fly with strong winds. Despite the major flight costs of wind action, birds did not fully optimize their flight track relative to wind direction, probably because of prey distributions relative to the coastline and wind predictability. Our study illustrates how both tortuosity and windscape shape the foraging costs of marine predators such as northern gannets.

KEY WORDS: Energetics, Accelerometry, State–space model, Foraging, Seabird, Wind

INTRODUCTION

Animal energetics play a central role in ecology by conditioning individual fitness, population processes and, ultimately, trophodynamics and ecosystem functioning (Brown et al., 1993). Energy balance is determined by energy expenditure and food acquisition, and optimal foraging theory predicts that animals should minimise the former while maximizing the latter (Bell, 1991). The study of energy expenditure in foraging animals is therefore particularly relevant, yet levels of energy expenditure associated with foraging are usually estimated using theoretical approaches or measured in small animals in captivity (McNab, 2002). Energetics studies in large and free-ranging animals are scarce, because of methodological challenges in recording simultaneously animal movements, energy expenditure and environmental variables that may influence movement costs. Wild animals can move on land, in water or in the air, and it is probably in the air that it is the most difficult to measure energy expenditure, because of technical limitations (Schmidt-Nielsen, 1972).

A vast body of work addresses the biomechanics of bird flight using theoretical and experimental approaches (Tobalske, 2007). The main limitations of experimental approaches performed in wind tunnels are that flight energetics are only measured in birds exposed to headwinds, which does not represent the whole range of wind directions encountered under natural conditions, and that conditions in wind tunnels are often turbulent, which can affect flight energetics (Pennycuick et al., 1997). In addition, studies concerning energetics of manoeuvring, performed under experimental conditions, are often not interpreted in the general context of foraging theory (e.g. Hedrick and Biewener, 2007; Su et al., 2012; but see Wilson et al., 2013). The prediction is that sinuous flight is more costly than straight flight because of the additional mechanical costs (Pennycuick, 1978), but this has never been tested empirically. To our knowledge, the energetic costs of turns have only been measured in humans (Minetti et al., 2011; Wilson et al., 2013). In a wider context, the cost of foraging movements can be measured either per time unit, considering that animals have to maximize their net energy intake per unit foraging time, or via their energy balance, because animals have to maximize the ratio of energy gained to energy spent (Ydenberg et al., 1994). Along these lines, the cost of tortuosity can be seen as the time it takes to cover a longer distance (Lusseau, 2004), or by an increase in the rate of energy expenditure while turning (Minetti et al., 2011; Wilson et al., 2013). Here we focus specifically on the latter aspect.

Until recently, it was very difficult to measure precisely the energy expenditure of free-ranging animals in real time. The doubly labelled water method allows the calculation of field metabolic rates but does not allow determination of energy expenditure over fine temporal scales (Shaffer, 2011). The first method used to this end consisted of equipping animals with loggers recording heart rate (Butler et al., 2004). This approach can be invasive for wild animals when it requires surgery, and can be hard to extrapolate if performed on captive animals, which do not have the same physical training as wild animals, and thus have different rates of energy consumption (Bevan et al., 1994; Ward et al., 2002). An alternative technique consists of equipping animals with three-axis accelerometers. This technique enables calculation of energy expenditure from dynamic body acceleration when the animal is active (Wilson et al., 2006), the main assumption being that energy expenditure is closely related

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List of symbols and abbreviations

AIC	Akaike's information criterion
A_x, A_y, A_z	acceleration on the x-, y- and z-axes
c	coefficient of variation
d	distance to the colony
d_{max}	maximum distance to the colony reached during the foraging trip
D_x, D_y, D_z	dynamic acceleration on the x-, y- and z-axes
ODBA	overall dynamic body acceleration
$ODBA_V$	mean vectorial ODBA per minute
SSM	state–space model
S_x, S_y, S_z	static acceleration on the x-, y- and z-axes
t	time elapsed
t_{max}	total duration of the foraging trip
μ	mean
ρ	precision

to mechanical work. Validations of this approach have been performed using oxygen consumption (Wilson et al., 2006), the doubly labelled water technique (Elliott et al., 2013) or heart rate measurements (Halsey et al., 2008). The limitation of the dynamic body acceleration technique is that it does not allow the estimation of energy expenditure resulting from basal metabolic rate, digestion or thermoregulation, although these values are easier to model than mechanical work (Gleiss et al., 2011). Yet its great practical advantage is that it can be easily measured in the field by attaching miniaturized electronic devices to wild, free-ranging animals.

Under natural conditions, the environment shapes the energy expenditure of foraging animals (Shepard et al., 2013). For example, walking on sand requires more energy than walking on a hard substrate in humans (Lejeune et al., 1998). And Rey and colleagues (Rey et al., 2010) found that, at sea, Magellanic penguins (*Spheniscus magellanicus*) take advantage of tidal currents to reduce commuting costs. For flying birds, wind speed and direction influence flight energy expenditure. For instance, the migration routes of Cory's shearwaters (*Calonectris diomedea*) are spatially determined by wind patterns (Felicísimo et al., 2008). Shearwaters follow a longer route in distance than a beeline, but it is probably less costly because of better wind conditions. Northern fulmars (*Fulmarus glacialis*) have higher field metabolic rates at low wind speeds, probably because of higher wing-beat frequency (Furness and Bryant, 1996). Finally, Weimerskirch et al. (Weimerskirch et al., 2000) found that the heart rate of wandering albatrosses (*Diomedea exulans*) was lower in birds exposed to tail winds. Recent studies have modelled energy landscapes, predicting the fine-scale energetic costs of moving in a given environment (Shepard et al., 2013; Wilson et al., 2012).

Considering the great ecological importance of flight energetics, the paucity of studies evaluating the energetic consequences of sinuous flight in foraging animals, and recent electronic developments allowing the monitoring of dynamic body acceleration in free-ranging, wild animals, we tested whether flight path tortuosity, as well as wind conditions, predicts flight energy expenditure.

Our study was conducted in foraging northern gannets [*Morus bassanus* (Linnaeus 1758)] during the breeding season. Northern gannets are the largest (180 cm wingspan) seabird species in the North Atlantic. They perform plunge-dives to catch fast-swimming pelagic fish such as mackerel (*Scombrus scomber*) and they gain height before plunging at high speeds. They usually remain within 10 m of the water surface, but can reach >20 m by actively swimming down through wing and leg movements (Garthe et al., 2000). They are flap-gliders, their flight being composed of small periods of flapping flight separated by glides. We therefore expected their energy expenditure to be correlated with the proportion of flapping versus gliding flight. Three typical behavioural states are observed during foraging trips: (1) a travelling state, when birds commute between the colony and prey patches or between prey patches; (2) a foraging state, when birds actively search for prey in a patch; and (3) a resting state, when birds sit on the water surface. Tortuosity is expected to be higher during foraging than during travelling or resting, because birds increase turning rate and reduce their speed as a response to prey detection or increased feeding rate (Fauchald and Tveraa, 2003). When prey have an aggregated spatial distribution, this predatory searching behaviour, termed area-restricted search, tends to concentrate the search activity of the predators in areas of relatively higher prey density (Kareiva and Odell, 1987). Conversely, outside feeding patches, commuting paths are expected to follow a straight line, for birds to minimise flight costs in poorer environments. Between the colony and the feeding areas, assuming that wind direction is constant during a trip, we expect that birds encounter wind from different angles (head, cross or tail wind) depending on outward or return phases. This may lead to different costs between outward and return journeys. We defined windscape as the wind dimension (wind force and direction) of a seascape, which integrates all physical parameters describing the marine environment in which our study species live.

We used GPS and acceleration data loggers attached to foraging northern gannets to test: (1) whether gannet energy expenditure is higher during foraging relative to travelling states because of higher tortuosity, taking windscape into account, (2) whether there is a difference in gannet energy expenditure between outward and return flights due to changes in wind direction, and (3) whether gannet energy expenditure is correlated to the number of wing beats per minute.

RESULTS

Analyses were conducted using GPS, accelerometer, dive and wind data collected from 19 breeding adults in June 2011 and 16 breeding adults in June 2012 during the chick-rearing period. We used the vectorial overall dynamic body acceleration ($ODBA_V$) calculated from accelerometry data as an index of energy expenditure per minute (see Materials and methods for calculation details). Bird trajectories and average wind conditions are represented in Fig. 1. Median wind speeds in the study area were slightly lower in 2012 than in 2011 (Fig. 1), whereas the main wind direction was comparable in both years (southwesterly winds).

Behavioural state assignment using state–space models

We inspected speed (equivalent to step length) and turn angle distributions for each individual to check whether state assignment was correct (Fig. 2A,B). This verification ensured that turn angle variance was higher for track sections identified as foraging compared with travelling (Fig. 2B). There was also a speed difference between the three states (Fig. 2A), with higher speeds during travelling than foraging, and during foraging relative to resting. One individual that performed a quick half-day trip was analysed with two states only as it never stopped to rest. We also checked state assignment on GPS tracks (Fig. 2C) to ensure that there were no inconsistencies between track shape and assigned behavioural states. Fig. 2C shows a typical foraging trip, composed of travelling segments, foraging periods and a long night-time resting period. Note that dives, inferred from depth recorder data (Fig. 2C), occurred mainly during foraging but also occasionally while travelling.

During their overall trips, northern gannets spent on average 50.2±14.8% of their time resting, 30.7±10.5% travelling and
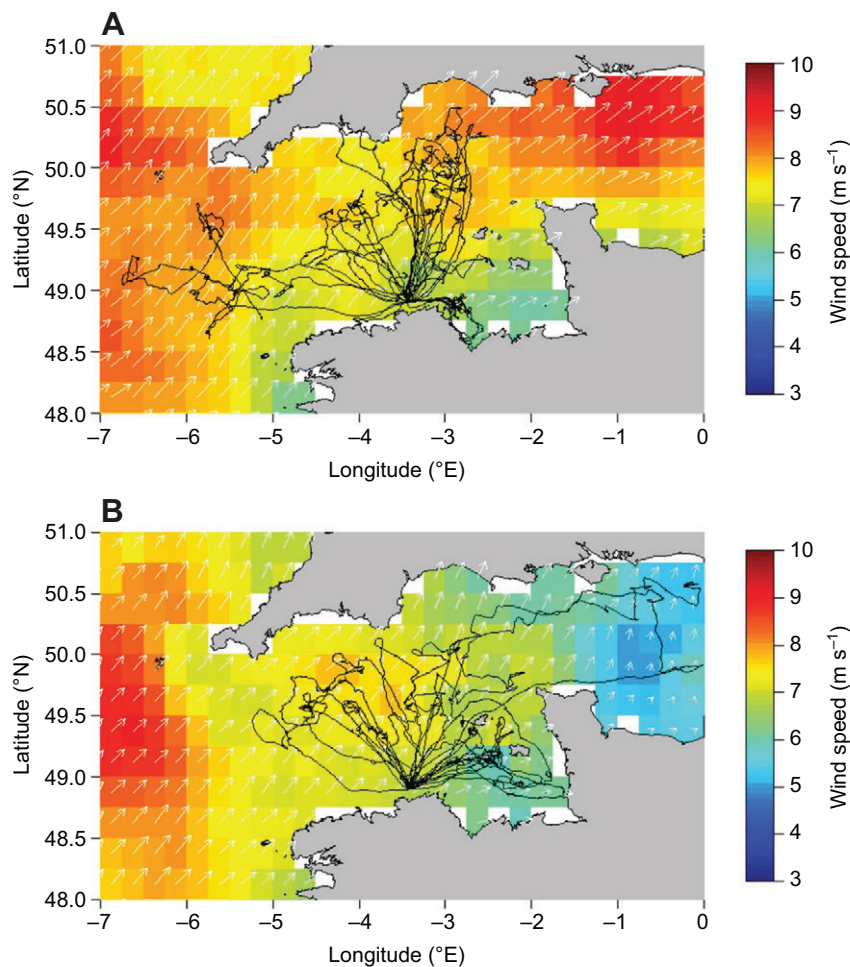
Fig. 1. GPS tracks overlaid on median wind speed and direction over the study period. Study periods were (A) 14–25 June 2011 (19 individuals) and (B) 12–23 June 2012 (16 individuals). Wind data are represented on a 0.25×0.25° grid (daily ASCAT surface wind speed, Cersat, Ifremer). White arrows represent wind direction and their length is proportional to wind speed.

19.0±10.9% foraging, respectively. Fig. 3 shows the distribution of $ODBA_V$ for each behavioural state. Despite our efforts to avoid inconsistencies in state assignment between foraging and resting (see Materials and methods), a limited number of resting periods were assigned to foraging (see the small peak on the left of the $ODBA_V$ distribution in foraging, Fig. 3B). To avoid biasing the analyses, we therefore excluded foraging $ODBA_V$ values smaller than the 85% quartile of the resting $ODBA_V$ distribution (solid red line, Fig. 3A,B, corresponding to 13.6% of the foraging values), because it is highly probable that these values actually corresponded to resting behaviour.

Effect of behavioural state and wind on $ODBA_V$

We first tested for differences in $ODBA_V$ between foraging and travelling states using a linear mixed-effect model with individuals as a random factor and a temporal autocorrelation structure. Wind speed and bird–wind angles were added as covariates because they were expected to influence $ODBA_V$. We also added sex and year because these variables possibly influenced energy expenditure.

Four models had a cumulative Akaike's information criterion (AIC) weight >0.90 (supplementary material Table S1A). All four models included an interaction between state, wind speed and bird–wind angle (supplementary material Table S1A). Model 1.1, with the smallest AIC, only included these three explanatory variables (supplementary material Table S1; AIC weight=0.43). The three other models additionally included sex and/or year as explanatory variables (supplementary material Table S1A; AIC weights between 0.11 and 0.27). As the increased complexity of the

fixed effect structure did not lead to an increase in goodness of fit (r_c=0.41 for all four top models), we chose to retain the simplest model (Model 1.1).

Prediction surfaces of Model 1.1 are represented in Fig. 4. They reveal that $ODBA_V$ was greater when birds were foraging, compared with travelling (state travelling effect: estimate ± s.e.m.=–0.045±0.014; Figs 3, 4). There was a negative effect of bird–wind angle and wind speed, $ODBA_V$ being lower with tail winds than with head winds and when wind speed increased. These wind effects were more pronounced during travelling than during foraging (Fig. 4).

As $ODBA_V$ was influenced by bird–wind angle, we investigated whether the proportion of bird–wind angles encountered during foraging and travelling differed. Frequency distributions of bird–wind angles in both states showed that birds spent more time with head winds while foraging (Fig. 5A). Frequency distributions of bird–wind angles were more homogenously spread during travelling, although there were fewer observations for tail winds (Fig. 5B).

### Effect of trip phase on $ODBA_V$ when travelling

Bird–wind angles differed greatly between outward, middle and return trip phases (Fig. 1, Fig. 5C,D). Indeed, birds spent more time flying with tail winds during the outward phase (Fig. 5C) and with head winds while returning to the colony (Fig. 5D). Bird–wind angle distribution was homogeneous during the middle phase of trips, with slightly more observations with head winds. We therefore decided to investigate whether there were some differences in energetic costs between these phases of the trips. We tested this hypothesis using a
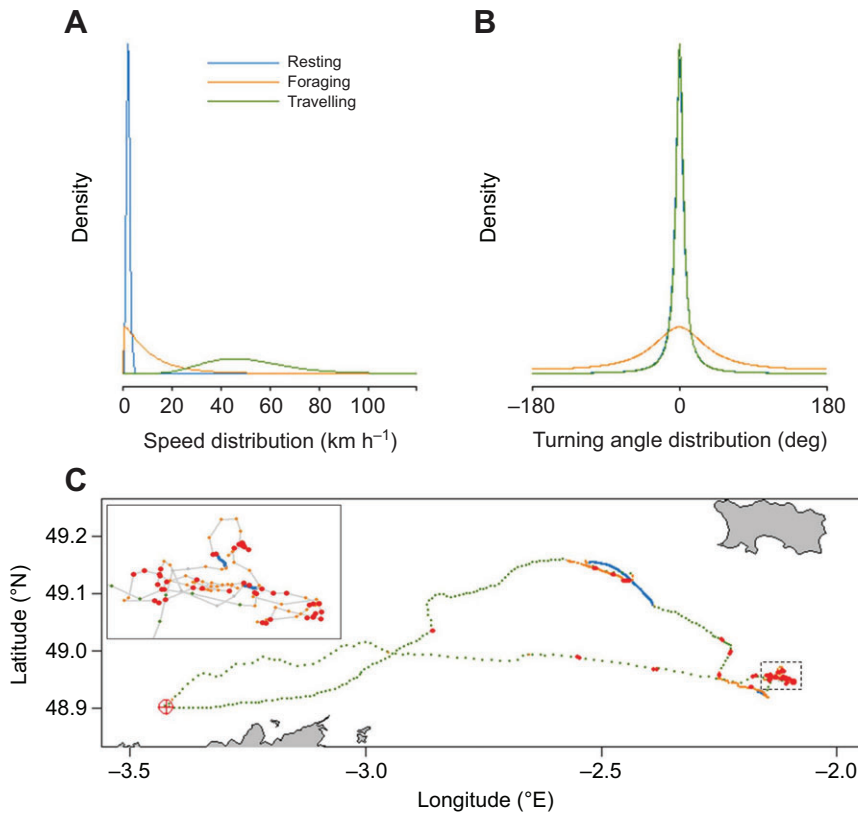
Fig. 2. Example of behavioural state assignment for one individual (foraging track with 1050 GPS locations). (A) Posterior distribution of speeds per state. (B) Posterior distribution of turning angles per state. (C) GPS positions re-interpolated at a constant time interval (60 s). Each colour represents the state assigned to a given location (blue for resting, orange for foraging and green for travelling). Red points represent positions where a dive occurred. The red crossed circle corresponds to the breeding colony. The foraging area delimited by the dotted rectangle is enlarged in the top-left corner.

linear mixed-effect model with $ODBA_V$ as a function of trip phase, year and sex (Model 2; supplementary material Table S2). Wind data were not added to the model; its effect was included in the trip phase effect. We used travelling phase data only to focus on the costs of commuting.

Four models had a cumulative AIC weight >0.90 (supplementary material Table S2A). All of them included trip phase. Model 2.1 with the lowest AIC (weight of the model: 0.43) only had trip phase as an explanatory variable. The three other models also had sex and/or year as explanatory variables (supplementary material
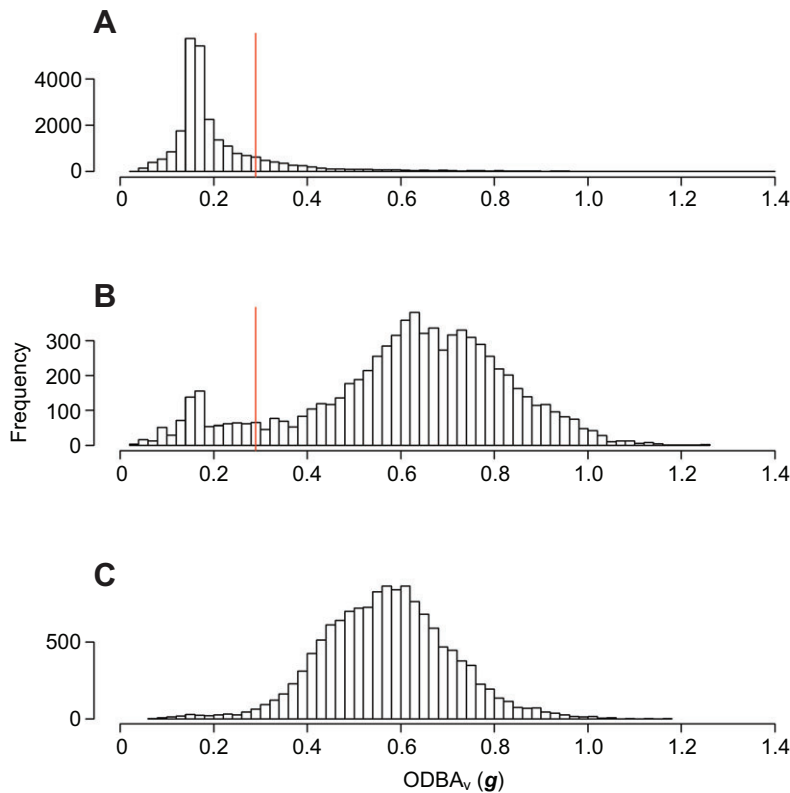
Fig. 3. Frequency distribution of vectorial overall dynamic body acceleration ($ODBA_V$) for each behavioural state. (A) Resting: 26,066 observations. (B) Foraging: 7906 observations. (C) Travelling: 14,352 observations. Red lines represent the 85% quartile of $ODBA_V$ distribution for the resting state. Values below this threshold in foraging state were considered as associated with resting, because of a slight inconsistency in state assignment (see Materials and methods).
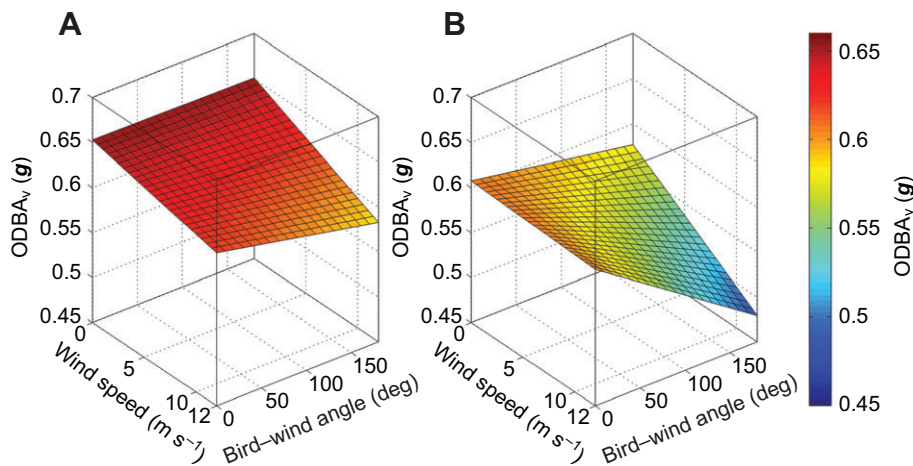
Fig. 4. Predicted effects of wind speed and bird–wind angle on ODBA$_V$ for foraging (A) and travelling (B) behavioural states. ODBA$_V$ is a proxy for energy expenditure calculated from acceleration data. Bird–wind angle is the angle between bird direction and wind origin; 0 deg corresponds to head wind and 180 deg to tail wind. Predictions were calculated from Model 1 (see supplementary material Table S1).

Table S2A; AIC weights of the models between 0.25 and 0.11). The four models had a goodness of fit equal to 0.38. Again, the complexity of the model did not increase the goodness of fit so we retained the simplest model (Model 2.1).

According to Model 2.1 (supplementary material Table S2B), ODBA$_V$ was higher during the return phase compared with the middle phase (middle phase effect: estimate ± s.e.m.=–0.023±0.006), and was higher during middle and return phases compared with the outward phase (outward phase effect: estimate ± s.e.m.=–0.043±0.007).

Effects of wing beats per minute on ODBA$_V$

We tested the effect of the number of wing beats per minute on ODBA$_V$. There was a strong, positive correlation between ODBA$_V$ and the number of wing beats per minute (Fig. 6; linear regression: $n=68$, $R^2=0.76$, $P<0.001$), which was not affected by sex. As northern gannets are flap-gliders, an increase in the number of beats per minute is not necessarily an increase in wing-beat frequency, but could also correspond to a shortening of gliding periods towards longer flapping periods. Bird turn angle had no effect on the number of wing beats per minute.

DISCUSSION

Using GPS, three-axis acceleration and dive data collected on northern gannets, we validate our hypothesis that energy expenditure per minute

is higher during sinuous foraging flights than during more rectilinear travelling. Our results are in accordance with optimal foraging theory predicting that sinuous movements are more costly than straight ones, because of additional mechanical costs (Pennycuick, 1978). Flight parameters (direction, speed) are more constant during travelling compared with during foraging. Crucially, we showed that such variability in flight parameters while foraging is associated with higher energetic costs (Fig. 4). As a consequence, commuting paths are expected to be straight in homogeneous environments outside feeding patches, to minimize energy expenditure and time investment.

To our knowledge, this is the first time that the cost of tortuosity has been measured in free-living animals other than humans (Minetti et al., 2011; Wilson et al., 2013). In birds, a series of field studies (some cited below) estimated 'true' flight costs, mainly using the doubly labelled water method, but at the scale of days. In great contrast our investigations estimated energy expenditure at a 1-min scale. We also confirm that windscape parameters (wind speed and direction) are important factors conditioning energy expenditure in foraging and travelling birds. Fig. 7 summarizes energetic costs of flight during a typical foraging trip.

Methodological limitations

Despite the great quality of the data used, our study has a series of caveats, which are addressed below.
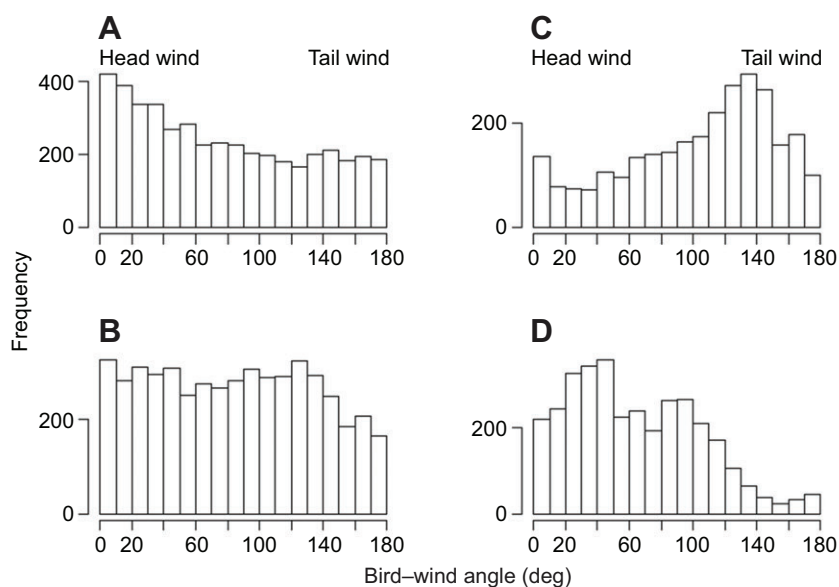
Fig. 5. Bird–wind angle distributions. Histogram of bird–wind angle distributions for foraging (A; 4450 observations) and travelling states (B; 12,246 observations), and for outward (C; 2814 observations) and return (D; 3357 observations) trip phases in travelling. Bird–wind angle is the angle between bird direction and wind origin. A and B correspond to the dataset used for Model 1. C and D correspond to the dataset used for Model 2.
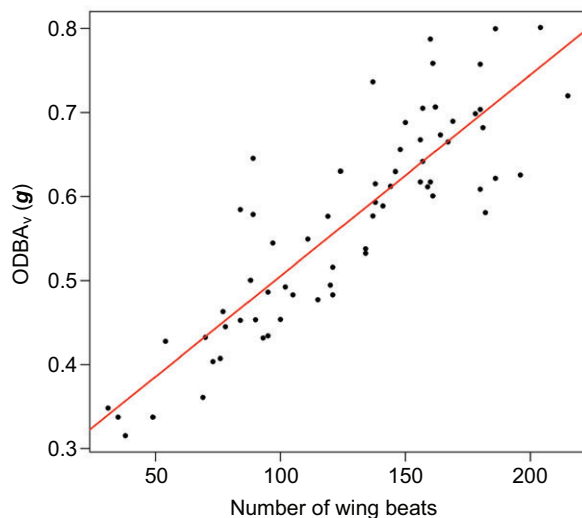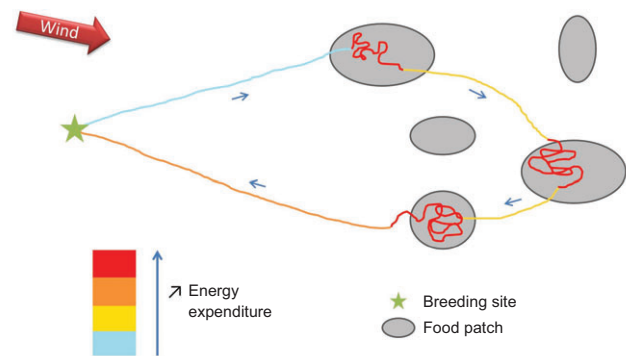
Fig. 6. Relationship between ODBA$_V$ and the number of wing beats performed per minute. The number of wing beats was counted in a random selection of 68 flight minutes (2 min per individual). The red line represents a linear regression ($n=68$, $R^2=0.76$, $P<0.001$).

Fig. 7. Schematic representation of the energetic costs of flight per minute for different portions of a northern gannet foraging trip. Energy expenditure per minute is highest during foraging phases within food patches. During travelling phases, energy expenditure per minute is higher for return trips that occur more often against the wind than for outward phases performed with the wind. Energy expenditure per minute of commuting phases between food patches is intermediate.

One potential limitation of our study was the temporal resolution of the GPS devices (1 min) compared with the duration of turns (seconds, or less). At this 1-min scale, the OBDA method allowed us to estimate average flight costs, but not to allocate these costs to specific movements. As estimated energy expenditure per minute is tightly linked to the number of wing beats per minute (Fig. 6), it is more than likely that turning is associated with more frequent wing flapping, but such wing flapping may occur before and/or after turns, the turning itself being performed in gliding flight. Direct observations of flying gannets should be performed to remove this ambiguity. Further, using a 1-min sampling interval does smooth the real flight path of the animal (Wilson et al., 2013). As a consequence, our bird–wind angle measurement was probably less accurate during foraging (when tortuosity is high) than during travelling, when flight bearing is more constant. Indeed, greater measurement error in covariates can bias downward, that is underestimate, the relationship between ODBA$_V$ and bird–wind angle. This may partly explain why the effect of bird–wind angle on energy expenditure was less pronounced during foraging (Fig. 4A). Conversely, using a higher sampling rate (such as one point per second) can lead to abnormal tortuosity because of inaccuracies in GPS positioning ($\approx 10\,\mathrm{m}$), something that can be problematic for behavioural state assignment. This was the main reason why a 1-min sampling interval was chosen.

Regarding windscapes, data obtained by remote sensing only give an approximation of actual wind speed and direction encountered by birds in flight, because of the spatial and temporal resolution inherent to satellite imagery. Indeed, the wind values that we used are daily averages over $0.25\times0.25°$ ($27.5\times27.5\,\mathrm{km}$) grid cells at 10 m height. Windscape most likely varies within one grid cell and within the 24 h period. Moreover, wind force varies also with height, and we did not take that into account as we did not know precisely at which height our birds flew (GPSs only provide very inaccurate altitude). Despite this lack of precision, windscape characteristics were highly significant in our models, highlighting their importance for energy expenditure levels.

Concerning differences in ODBA$_V$ between outward and return flights, we could not take into account the fact that birds were heavier on their way back because of food load. Firstly, it was not

possible to evaluate mass gain due to food load for birds returning to the colony because they often fed their chick before recapture. Secondly, this mass gain cannot be easily modelled because gannets spend long periods sitting on the sea surface along their trip, during which they partly digest their prey (Ropert-Coudert et al., 2004). Therefore, mass gain through food load is likely to occur to varying degrees during different phases of the trip, yet predominantly during return flight. This extra load does increase energy expenditure per minute (Wilson et al., 2006) and may also bias the effect of wind direction on ODBA$_V$, as unloaded birds flew preferentially with tail winds and loaded birds with head winds (Fig. 5C,D).

Further, we have to keep in mind that foraging and travelling behavioural states were inferred not only from turn angle but also from speed criteria. Speeds were much lower during foraging than travelling (Fig. 2A). Such lower speed during foraging is partly due to the time spent diving and resting at the water surface just after the dives. We did not test whether speed during actual flight periods was significantly slower during foraging compared with travelling, as flying at lower speeds may be advantageous when detecting fish before diving. If it is the case, this must induce additional energetic costs at low speeds and contribute to the difference in energy expenditure per minute observed between foraging and travelling, as studies on mechanical costs of flight in birds have measured that power costs of flight follow a U-shape function as velocity increases (reviewed in Tobalske, 2007).

Finally, we intentionally removed dives and take-offs from our data and analyses so as to focus exclusively on flight periods. Yet take-offs are known to result in increased energetic costs, especially at low wind speeds. For instance, in wandering albatrosses (*Diomedea exulans*), which are gliders, take-offs and landings are energetically the most costly periods at sea (Shaffer et al., 2001; Weimerskirch et al., 2000). As dives are more numerous during foraging than during travelling, the costs of take-offs are expected to enhance the difference in energy expenditure between these two states. There may also be a cost associated with gaining height before performing a plunge dive.

Wind-speed effect on energy expenditure depends on flight style

Relationships between daily energy expenditure measured using the doubly labelled water method and wind speed vary greatly between

species (Furness and Bryant, 1996). The main reason appears to be flight style, related to wing morphology (Spear and Ainley, 1997). Pure flappers such as black-legged kittiwakes (*Rissa tridactyla*) and little auks (*Alle alle*) spend more energy in flight when wind speed increases (Gabrielsen et al., 1987; Gabrielsen et al., 1991). As a consequence, the growth rate of little auk chicks decreased when their parents were exposed to higher wind speeds at sea (Konarzewski and Taylor, 1989). On the contrary, in northern fulmars (*Fulmarus glacialis*), which are flap-gliders, energy expenditure decreased as wind speed increased (Furness and Bryant, 1996). In this case, wing-beat frequency tends to increase when wind is slack. Similarly, global warming causing higher average wind speeds in the Southern Ocean has been shown to favour foraging efficiency and enhance breeding success in wandering albatrosses (Weimerskirch et al., 2012). Surprisingly, Cape gannets (*Morus capensis*), which are closely related to northern gannets, showed higher daily energy expenditures at higher wind speeds (Mullers et al., 2009). Such measurements seem contrary to our findings. However, because they were performed at the scale of days instead of minutes, they are not directly comparable: it is for instance possible that Cape gannet foraging success was lower at high wind speeds, because of rippling of the sea surface, reducing prey visibility (Finney et al., 1999). This could force Cape gannets to perform more dives, thereby increasing overall daily energy expenditure, even if their flight costs per unit time were lower than at lower wind speeds.

Head winds increase flight costs

We observed a decrease in energy expenditure per minute when bird–wind angles increased (i.e. when they flew with the wind), particularly during travelling phases. These results corroborate findings by Weimerskirch et al. (Weimerskirch et al., 2000) on gliding wandering albatrosses in the Southern Ocean. Conversely, flight costs increased when birds faced the wind, something that is likely to result from higher flapping flight proportion to the detriment of gliding flight (Fig. 6) (Sakamoto et al., 2013). Theoretically, there is no reason for birds to spend more energy per minute with head winds than with tail winds; the only difference will be their speed. As a consequence, the global cost of transport is expected to increase with head winds as more time will be needed to cover the same distance. It is possible that northern gannets compensate for the slowing down effect of head winds by flying faster, and thus increasing their energy expenditure per minute, so as to come back in time to the colony to feed their chicks. Not only energy but also time spent away from the nest is a currency that chick-rearing seabirds need to optimize (Stephens and Krebs, 1986).

It is surprising that northern gannets spent a high proportion of time with head winds while foraging, as it is more costly (Fig. 5A). This may be a consequence of the numerous take-offs following dives, which typically occur against the wind. Another possibility is that birds flew against the wind while foraging to reduce speed, which can be advantageous to detect prey visually (Machovsky-Capuska et al., 2012). Lastly, northern gannets may also use olfaction to search for prey. In this case, an upwind approach is necessary to fly against smell dispersion, as in the wandering albatross (Nevitt et al., 2008).

We found that gannets tended to fly with the wind during outward journeys, and to fly back to the colony against the wind (Fig. 5C,D). The same results were found during previous studies of central-place foraging seabirds. For instance, common guillemots (*Uria aalge*) from the Baltic Sea (Evans et al., 2013) and sooty shearwaters (*Puffinus griseus*) off New Zealand (Raymond et al., 2010) also left the colony with tail winds and came back with head winds. Flying against the

wind on the way back to the breeding colony is particularly costly because birds are then carrying additional food loads for their offspring. This extra load was found to significantly increase energy expenditure during return trip phases in great cormorants (*Phalacrocorax carbo*) (Wilson et al., 2006). For northern gannets, our observations are therefore not in accordance with optimal foraging theory, which predicts that the forager should optimise wind use to minimise energy expenditure during return trips.

One possible explanation is that birds cannot predict wind conditions along their foraging trip. If they have no *a priori* knowledge about future wind fields when they leave the colony, it is more advantageous for them to leave with favourable wind conditions. If wind conditions are changing quickly, they have a chance to take advantage of tail winds during both outward and inward routes. In more predictable environments, birds take full advantage of favourable conditions. For example, condors follow windward slopes to use air ascendance and thus reduce their flight costs and optimize their route depending on wind direction (Shepard et al., 2013). We also propose that gannets from the English Channel do not comply with theory because their flying directions are strongly constrained by coastlines and because they do not breed on an oceanic island. This is the case for wandering albatrosses, which take advantage of winds in the extreme. As their insular breeding site is very small and isolated, their flight ranges are not constrained by any coastline. Further, they travel in very large loops (>1000 km) to take advantage of wind directions that vary regionally in the Indian and Southern Oceans, avoiding head winds more or less completely (Weimerskirch et al., 2000). Consequently, the travels of wandering albatrosses in the Southern Ocean are far less repeatable than those of northern gannets in the English Channel, which have been shown to anticipate the location of the targeted feeding site soon after leaving their breeding colony (Pettex et al., 2010) and to use the same feeding grounds repeatedly (Patrick et al., 2013). Just as the coastline and prevailing southwesterly winds (Fig. 1), localized, stable prey patches probably also strongly constrain gannet flying directions, and therefore their flight directions relative to the wind.

In conclusion, our study shows higher flight costs in northern gannets while foraging compared with travelling. Yet we also clearly identify windscape as a component strongly shaping the flight costs of northern gannets. Travelling at low wind speeds can therefore be more costly than foraging at high wind speeds. This clearly illustrates how wind speed and direction shape the seascape of marine predators, just as landscape affects the movement costs of terrestrial animals (Wall et al., 2006).

MATERIALS AND METHODS
Fieldwork
Field protocols were validated with respect to ethics in animal experimentation by the French Direction des Services Vétérinaires (permit no. 34-369). Northern gannets were equipped with data-loggers on Rouzic Island, Sept Iles Archipelago, Brittany (48°54′0″N, 3°26′11″W; ~20,000 breeding pairs), in 2011 (22 individuals) and in 2012 (27 individuals) during the chick-rearing period. Breeding adults were caught at the nest when both parents were present, using a telescopic pole fitted with a metal crook. Each bird was equipped with a GPS logger (CatTraQ™, Catnip Technologies, Hong Kong, China; 47×30×13 mm, 20 g) and a three-axis accelerometer (G6A, CEFAS Technology Limited, Lowestoft, UK; 40×28×15 mm, 18 g), which also recorded hydrostatic pressure as an index of dive depth. GPS loggers recorded location every 30 s while accelerometers recorded temperature and depth every second, as well as acceleration in three axes at 20 Hz. These two devices together weighed less than 1.3% of the bird's body mass. They were attached with white Tesa® tape (Hamburg, Germany) on the lower back of the bird for the GPS and under the central tail feathers for

the accelerometer. Handling lasted less than 10 min. In 2011, all birds but one were recaptured. In 2012, three birds were not recaptured and one lost its GPS unit. For nine accelerometers, data were unusable because of a malfunction of the pressure sensor. In total, analyses were conducted on data from 19 birds in 2011 and 16 in 2012. Most of the birds were equipped for a single trip at sea (mean duration 22.6±10.7 h), while three were recaptured after two trips. In this case, the second trip was not included in the analyses to avoid pseudoreplication. Previous investigations showed very high repeatability in foraging behaviour across successive trips, justifying the assumption that the first trip is representative of individual foraging behaviour (Patrick et al., 2013). Northern gannets are monomorphic, and the sex of the equipped birds was determined from blood samples collected upon recapture and recovery of all electronic devices.

GPS data analyses: behavioural state assignment

As the time interval between two GPS locations was not strictly constant in our dataset, tracks were re-interpolated at a constant time interval of 1 min. For each GPS position, we calculated step length (m) and turn angle (deg), which is the angle between two successive path steps. The turn angle is equal to 0 if the path is straight and equal to π if the bird makes a U-turn (Calenge et al., 2009).

Discrete behavioural modes were inferred from step length and turn angle data using a state–space model (SSM) adapted from the triple switch model (Morales et al., 2004). This method allows estimation of a sequence of states in animal tracking data when behaviour itself is not directly observable. Three different states were defined: resting (small step length, small turn angle variance), travelling (large step length, small turn angle variance) and foraging (medium step length, high turn angle variance). SSM output provides the probability to be in a given state at each GPS position.

Step length distribution was modelled using a Gamma likelihood function, with mean μ and coefficient of variation c:

$$G\left(\text{shape} = \frac{1}{c^2}, \text{ rate} = \frac{1}{\mu c^2}\right). \qquad (1)$$

Thus, we could implement the following identification constraint: $\mu_{resting} < \mu_{foraging} < \mu_{travelling}$. We used an exponential prior for both the mean and the coefficient of variation. The prior for the coefficient of variation was informative, favouring values smaller than 1 to ensure a unimodal distribution. The likelihood for turning angles was a wrapped Cauchy distribution (Morales et al., 2004): wC(mean=θ, precision=ρ). We used the following constraint on turning angle precision parameters: $\rho_{resting} > \rho_{foraging} < \rho_{travelling}$, to ensure that foraging was associated with a larger variance. The models were fitted using Markov chain Monte Carlo methods implemented in JAGS (Plummer, 2003) called from R version 2.15.2 (R Development Core Team, 2013) using the library Rjags. We ran six chains with overdispersed starting values for a burn-in of 40,000 iterations. We then ran 10,000 further iterations, storing one iteration out of 10 for posterior inference (i.e. the final sample size is 1000 iterations per chain). Convergence was assessed visually and with Gelman–Brooks–Rubin statistics (Cowles and Carlin, 1996). Inference was made from at least three converging chains. We also checked pseudo-residuals as defined in Patterson et al. (Patterson et al., 2009).

Trip phase calculation

Each foraging trip was divided into three phases: outward, middle and return. To define transitions, we followed Wakefield et al. (Wakefield et al., 2009): for each GPS position, we calculated the distance to the colony divided by the maximum distance to the colony reached during the foraging trip (d/d_{max}) and the time elapsed divided by the total duration of the foraging trip (t/t_{max}). Then we plotted d/d_{max} against t/t_{max}. We visually determined the limits of the outward and return phases, which are characterized by two breakpoints. These breakpoints delimit a phase with a high commuting rate (either outward or return phase) where d/d_{max} varies rapidly, and a middle phase where d/d_{max} stabilizes.

ODBA calculation

Acceleration data, in $\boldsymbol{g}$, were analyzed with the software Igor Pro version 6.31 (Wavemetrics, Portland, OR, USA). ODBA is a measure of body

motion derived from measurements of acceleration along all three spatial axes (Wilson et al., 2006). This measure of the mechanical work performed by individuals can be used as a proxy for energy expenditure under certain conditions (Halsey et al., 2011). ODBA was calculated as described in Wilson et al. (Wilson et al., 2006) and Shepard et al. (Shepard et al., 2008). Acceleration (A) is the sum of static acceleration (S) resulting from body angle with respect to gravity and dynamic acceleration (D) resulting from body movements, i.e. $A=S+D$. First, for each axis, we calculated S, which has a running mean of 2 s, using the box smooth function with 39 points in Igor Pro. To choose an appropriate duration for the smoothing, the time interval of 2 s for the running mean was determined by a calibration made during 1-min periods of constant flapping flight, following Shepard et al. (Shepard et al., 2008).

Two formulae are commonly used to calculate ODBA:

$$\text{ODBA}_{\text{vectorial}} = \sqrt{(A_x - S_x)^2 + (A_y - S_y)^2 + (A_z - S_z)^2}, \qquad (2)$$

$$\text{ODBA}_{\text{sum}} = |A_x - S_x| + |A_y - S_y| + |A_z - S_z|. \qquad (3)$$

We chose to use OBDA$_{\text{vectorial}}$ and not OBDA$_{\text{sum}}$ for the statistical analyses because OBDA$_{\text{vectorial}}$ is less sensitive to small changes in logger position on the birds (Gleiss et al., 2011). Finally, we calculated mean OBDA$_{\text{vectorial}}$ per minute to match with GPS data, and we shortened this term to 'ODBA$_V$' for the rest of the article.

When comparing acceleration data with the output of the SSMs, we detected a recurrent inconsistency in state assignment: some periods of obvious resting (according to the position of the bird and minimal ODBA$_V$ values) were classified as foraging when turn angles varied (such as during tidal reversion). To correct for this, we used the static acceleration of the x-axis (S_x), corresponding to the antero-posterior axis of the bird, for which values were different when the bird was flying or sitting on water, showing a bimodal distribution. Periods of foraging during which S_x corresponded to a bird sitting on water were therefore forced into the resting state.

Diving data analyses

Diving data were processed using the program divesum [Grant Ballard, unpublished software; see Lescroël et al. (Lescroël et al., 2010) for more details]. This program corrected the baseline record and computed several individual dive parameters such as start time, maximum dive depth, dive and post-dive interval durations. Only dives ≥0.5 m deep and ≥1 s long were considered. Minutes during which a dive occurred and minutes following a minute with a dive (which included the short resting period following a dive and the take-off phase) were excluded from the analyses of ODBA so that the number of dives would not influence the comparison of mechanical work during flight between behavioural states. From a random sample of 50 dives across all individuals, the mean dive cycle duration, calculated from the beginning of the rise in the air before the dive to the end of the take-off, was 22.6±10.3 s.

Windscape data

Daily windscape data were downloaded from the CERSAT portal (cersat.ifremer.fr, Ifremer, Plouzané, France). These data correspond to measurements from Metop/ASCAT satellite scatterometers and represent an estimate of the wind vector at 10 m height with a resolution of 0.25° in longitude and latitude. For each GPS position, wind speed and eastward and northward wind components were extracted from the corresponding grid cell. We then calculated the angle between bird direction and wind origin (bird–wind angle) at each time step along the trajectories.

Wing-beat count

To test the hypothesis that a higher energy expenditure results from more wing beats per minute, we counted the number of wing beats visible on the dorso-ventral axis of the accelerometer in 68 randomly chosen minutes (two per individual) of flight (minutes of foraging and travelling excluding dives). A linear regression was performed to quantify the relationship between ODBA$_V$ and wing beats per minute.

Molecular sexing

Blood (0.2 to 0.8 ml) was drawn from the tarsal vein and immediately centrifuged. Plasma and red cells were kept frozen separately in alcohol. DNA was extracted from the red cells with a DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). A PCR was performed with the primers 2550F and 27181R (Fridolfsson and Ellegren, 1999). DNA fragments were separated with electrophoresis on a 3% agarose gel with GelRed for visualization. Males have one band (ZZ) while females have two (WZ).

Statistical analyses

All the statistical analyses were performed using R version 2.15.2 (R Development Core Team, 2013) and followed methods described in Zuur et al. (Zuur et al., 2009). To model $ODBA_V$ as a function of state or tortuosity, wind speed, year and sex, we used linear mixed-effects models implemented within the nlme package (Pinheiro et al., 2013). As our dataset had repeated measurements for each individual corresponding to successive GPS locations along its trip at sea, we added bird identity as a random effect. To take into account serial autocorrelation due to repeated measurements in time, we used a first-order autocorrelation structure for the time, with the individual as a grouping factor.

First, starting with the most complete fixed-effects structure, we selected the best random effect structure by comparing models with different random effect structures (individual random effect and/or autocorrelation) using restricted maximum likelihood estimation. Then, we selected the best fixed-effect structure with the maximum likelihood method, starting with the most complete structure and testing all combinations of factors. Models were selected using AIC weights (Symonds and Moussalli, 2011) equal to:

$$\text{AIC weight}_{\text{model } i} = \frac{e^{-0.5\Delta\text{AIC}_i}}{\sum \left(e^{-0.5\Delta\text{AIC}}\right)}. \qquad (4)$$

AIC weight is a value between 0 and 1 analogous to the probability that a given model is the best approximating model. We selected models with the highest AIC weights until the cumulative weight exceeded 0.90. Among these models, the best one was selected depending on the complexity of the fixed-effects structure (number of parameters K) and the goodness of fit for linear mixed-effects models [r_c, see Vonesh et al. (Vonesh et al., 1996) for the formula]. The goodness of fit is interpretable as a concordance correlation coefficient between observed and predicted values. We graphically checked the selected models for homogeneity, independence and normality of the residuals (Zuur et al., 2009).

Author contributions

D.G., A.L. and C.P. conceived and designed the experiments. D.G., A.L., C.P. and P.P. performed the experiments. F.A., C.P., A.L. and M.A. analysed the data. F.A., D.G., C.P. and A.L. wrote the manuscript.

Supplementary material

Supplementary material available online at
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Table S1: Model selection using linear mixed-effect models and Akaike information criterion to test for the effects of state, wind speed, bird-wind angle (BWA), year and sex on ODBA$_V$. Not all models are represented. Table S1A present the selection of models with a cumulative sum of AIC weights>0.9 and the null model (intercept). Table S1B is the estimates of each best model with the lowest AIC. K is the number of parameters. ΔAIC is the difference of AIC between a given model and the model with the lowest AIC. AIC weight is the probability that a given model is the best approximating model.

S1A Model 1 selection (34 birds, 16696 locations)

N°	Model	K	AIC	ΔAIC	AIC weight
1.1	**State*WindSpeed*BWA**	**9**	**-31597.64**	**0**	**0.40**
1.2	Year+State*WindSpeed*BWA	10	-31596.7	0.94	0.25
1.3	Sex+State*WindSpeed*BWA	10	-31595.98	1.66	0.17
1.4	Year+Sex+State*WindSpeed*BWA	11	-31594.98	2.66	0.11
1.0	Intercept	2	-31082.76	514.88	0.00

S1B Model 1.1 parameter estimation

	Parameter	Estimate	SE
1.1	Intercept	0.653	0.018
1.1	StateTravelling	-0.045	0.014
1.1	WindSpeed	-0.0027	0.0020
1.1	WindSpeed:StateTravelling	0.0022	0.0019
1.1	BWA	-0.000011	0.000083
1.1	BWA:StateTravelling	-0.00016	0.00012
1.1	WindSpeed:BWA	-0.000016	0.000011
1.1	WindSpeed:BWA:StateTravelling	-0.000026	0.000017

1 **Table S2: Model selection using linear mixed-effect models and Akaike information criterion to**

2 **test for the effects of trip phase, year and sex on ODBA$_V$ during travelling.** Not all models are

3 represented. Table S2A present the selection of models with a cumulative sum of AIC weights >0.9

4 and the null model (intercept). Table S2B is the estimates of each best model with the lowest AIC. K

5 is the number of parameters. ΔAIC is the difference of AIC between a given model and the model

6 with the lowest AIC. AIC weight is the probability that a given model is the best approximating

7 model.

S2A Model 2 selection (32 birds, 11244 locations)

N°	Model	K	AIC	ΔAIC	AIC weight
2.1	**TripPhase**	**3**	**-24502.54**	**0**	**0.43**
2.2	Year+TripPhase	4	-24501.47	1.07	0.25
2.3	Sex+TripPhase	4	-24501.06	1.48	0.21
2.4	Year+Sex+TripPhase	5	-24499.85	2.69	0.11
2.0	Intercept	2	-24470.42	32.12	0.00

S2B Model 2.1 parameter estimation

	Parameter	Estimate	SE
2.1	Intercept	0.591	0.012
2.1	Middle Phase	-0.023	0.006
2.1	Outward Phase	-0.043	0.007

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