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Wind field and sex constrain the flight speeds of central-place foraging albatrosses

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Abstract. By extracting energy from the highly dynamic wind and wave fields that typify pelagic habitats, albatrosses are able to proceed almost exclusively by gliding flight. Although energetic costs of gliding are low, enabling breeding albatrosses to forage hundreds to thousands of kilometers from their colonies, these and time costs vary with relative wind direction. This causes albatrosses in some areas to route provisioning trips to avoid headwind flight, potentially limiting habitat accessibility during the breeding season. In addition, because female albatrosses have lower wing loadings than males, it has been argued that they are better adapted to flight in light winds, leading to sexual segregation of foraging areas. We used satellite telemetry and immersion logger data to quantify the effects of relative wind speed, sex, breeding stage, and trip stage on the ground speeds (V_g) of four species of Southern Ocean albatrosses breeding at South Georgia. V_g was linearly related to the wind speed component in the direction of flight (V_{wf}), its effect being greatest on Wandering Albatrosses *Diomedea exulans*, followed by Black-browed Albatrosses *Thalassarche melanophrys*, Light-mantled Sooty Albatrosses *Phoebastria palpebrata*, and Gray-headed Albatrosses *T. chrysostoma*. Ground speeds at $V_{wf} = 0$ were similar to airspeeds predicted by aerodynamic theory and were higher in males than in females. However, we found no evidence that this led to sexual segregation, as males and females experienced comparable wind speeds during foraging trips. Black-browed, Gray-headed, and Light-mantled Sooty Albatrosses did not engage in direct, uninterrupted bouts of flight on moonless nights, but Wandering Albatrosses attained comparable V_g night and day, regardless of lunar phase. Relative flight direction was more important in determining V_g than absolute wind speed. When birds were less constrained in the middle stage of foraging trips, all species flew predominantly across the wind. However, in some instances, commuting birds encountered headwinds during outward trips and tail winds on their return, with the result that V_g was 1.0–3.4 m/s faster during return trips. This, we hypothesize, could result from constraints imposed by the location of prey resources relative to the colony at South Georgia or could represent an energy optimization strategy.

Key words: albatrosses; ARGOS errors; central-place foraging; dynamic or gust soaring; flight speed; habitat preference; niche specialization; platform terminal transmitters, PTT; satellite tracking; seabird; sexual segregation; South Georgia.

INTRODUCTION

During the breeding season, pelagic seabirds have to return to their colonies at regular intervals and thus act as central-place foragers. One of the most extreme examples of this behavior is manifest in albatrosses (family Diomedidae), whose foraging trips may take them hundreds or thousands of kilometers from their colonies to remote patches of habitat, which are preferred due to high productivity or niche specialization (Nel et al. 2001, Hyrenbach et al. 2002, Phillips et

al. 2005, Pinaud and Weimerskirch 2005). Because of the great distances involved, the success of this strategy lies in maintaining relatively low transport costs while ensuring that trips, particularly those to provision chicks, can be completed within given time constraints. During flight, the metabolic rates of albatrosses are exceptionally low (Bevan et al. 1995, Arnould et al. 1996). This is because they proceed almost exclusively by gliding, which is the least energetically demanding form of flight (Pennycuik 1982, Norberg 1985). Although the exact mechanisms that albatrosses use to glide are still under debate, they are thought to rely predominantly on exploiting wind velocity gradients close to the surface of the sea (“gust” or “dynamic soaring”; Tickell 2000, Pennycuik 2002).

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Wind also plays a major role in dictating flight patterns at larger spatial scales. Satellite tracking has shown that some species tend to direct their flight paths relative to synoptic-scale wind patterns, avoiding headwind flight (Weimerskirch et al. 2000b, Murray et al. 2003). However, many areas traversed by albatrosses are subject to strong, persistent prevailing winds. In such areas birds traveling to and from foraging patches may be more constrained in their choice of flight directions. This is of considerable consequence because albatrosses rarely resort to flapping flight (Pennycuik 1982); thus their ground speeds and, hence, transport costs are likely to be affected by their orientation with respect to the wind at several spatial scales.

The ability to regulate flight speed may be particularly important for breeding birds (Hedenström and Ålerstam 1995). Albatrosses, like all seabirds, experience changes in the severity of the central-place constraint as the breeding season advances (Shaffer et al. 2003). During incubation, which is carried out alternately by both parents, foraging trips may be long, their duration limited only by the fasting capability of the bird left on the nest (Weimerskirch 1995). After hatching, the chick is brooded or guarded for a few days or weeks (depending on the species) alternately by one parent while the other forages. Thereafter, it is left unattended and provisioned by both parents. During these latter stages, the length of foraging trips is usually much shorter because adults must satisfy both their own and their chicks' energetic requirements (Weimerskirch et al. 1997a). Although several studies have shown that albatrosses contract their foraging ranges in response to these changing time constraints (Shaffer et al. 2003, Phillips et al. 2004), the hypothesis that they also regulate ground speeds in order to reduce time costs during more constrained stages, by changing flight direction with respect to wind direction, has not been tested. Furthermore, within individual foraging trips it is likely that ground speeds, measured at the scale of hours, will vary with behavior. For example, birds en route to and from foraging areas are likely to travel faster than those engaged in prey search and capture (Houston 2006).

The airspeed, and therefore ground speed, of gliding birds is also constrained by their morphology. Theoretical airspeed is proportional to the square root of a bird's wing loading (defined as the mass per unit wing area; Pennycuik 1989). Wing loadings are greater in the larger species of albatross (Shaffer et al. 2001, Phillips et al. 2004), in theory resulting in greater airspeeds. Furthermore, because albatrosses are sexually size dimorphic, theoretical airspeeds of females are lower than those of males. This prediction has led to the hypothesis that females have concomitantly lower stall speeds due to adaptation to flight in light winds, which explains the pattern of spatial sexual segregation observed in some species (Shaffer et al. 2001, Phillips et al. 2004). However, empirical relationships between

ground speeds of males and females and wind speed and direction have not hitherto been tested.

In this paper we examine several factors that may influence flight speeds of foraging albatrosses. First, we use a combination of satellite telemetry and immersion logger data to quantify ground speeds of Wandering Albatrosses *Diomedea exulans*, Black-browed Albatrosses *Thalassarche melanophrys*, Gray-headed Albatrosses *T. chrysostoma*, and Light-mantled Sooty Albatrosses *Phoebastria palpebrata* at the scale of hours. We chose these species because they breed sympatrically and reflect the range of sizes and life history traits expressed by albatrosses. By careful selection of tracking locations, we minimize errors in ground speed estimates, allowing us to model the response to relative wind speed. We compare observed interspecific and sexual differences in ground speeds with those predicted by aerodynamic theory, testing the hypotheses that larger species fly faster than smaller ones. For each species, we then model ground speed in response to relative wind speed in more detail, considering the effects of breeding and trip stage, and testing the hypothesis that males fly faster than females. Because albatrosses are more active during the day and on moonlit nights (Weimerskirch and Guionnet 2002, Phalan et al. 2007), we also consider whether diel or lunar phase could influence our estimates of ground speed. We then test the hypothesis that male birds frequent windier habitats than females. Finally, we compare observed flight directions with respect to wind during the outward and inward stages of foraging trips, when birds are more constrained in their choice of flight directions, and between species during the comparatively unconstrained middle stages of trips.

METHODS

Instrumentation

Albatrosses were tracked from Bird Island, South Georgia (54°00' S, 38°03' W) during the austral breeding seasons of 2000/2001–2003/2004 (see Appendix A for full deployment details). A total of 52 Black-browed Albatrosses, 47 Gray-headed Albatrosses, and 4 Light-mantled Sooty Albatrosses were equipped with PTT 100 Platform Terminal Transmitters (either 20 g, 54 × 18 × 17 mm or 30 g, 63 × 18 × 17 mm; Microwave Telemetry, Columbia, Maryland, USA) set to transmit about every 90 s. Locations were received from these devices, on average, every 1.13 h. In addition, 54 Wandering Albatrosses were equipped with BGDL-II GPS loggers (67 g, 42 × 71 × 31 mm; Fukuda et al. 2004) set to log positions at intervals of 0.5 to 2 h. All birds were of known sex, except the Light-mantled Sooty Albatrosses, and approximately equal numbers of males and females were tracked. In some cases data were collected from individual birds during several consecutive foraging trips. For the purposes of comparison between taxa, PTT and GPS data were subsampled by removing intervening locations, such that the mean location interval ranged from 2.37 to 2.75 h (Appendix A). Most

birds also carried a British Antarctic Survey Mk IIa–IV logger (5 g, $8 \times 18 \times 25$ mm or 10 g, $12 \times 19 \times 22$ mm; Afanasyev and Prince 1993) or a Francis Scientific Instruments saltwater activity logger (17 g, $10 \times 10 \times 30$ mm; Francis Scientific Instruments, Cambridge, UK). These recorded saltwater activity (immersion), either as the total number of wet values in 10-min blocks sampled every 3 s or wet–dry status at intervals of 10 s. Data from both types of device were standardized to the proportion of time wet in 10-min blocks (Phalan et al. 2007). In all cases, birds were captured at the nest, either by hand or using a 1.5-m pole fitted with a wire crook, and were equipped with loggers in a procedure that took <10 min. GPS loggers and PTTs were attached to mantle feathers using Tesa tape (Tesa UK, Milton Keynes, Buckinghamshire, UK), while immersion loggers were attached with cable ties to plastic rings placed around the tarsus. Total instrument mass (including attachment materials) as a percentage of average body mass was 0.6% for Wandering Albatrosses (range 0.5–0.7%); 1.5% for Black-browed Albatrosses (range 1.2–1.9%); 1.6% for Gray-headed Albatrosses (range 1.3–1.9%); and 2.0% for Light-mantled Sooty Albatrosses (range 1.8–2.4%). Thus, in all cases instrumentation mass was well within recommended limits of $\leq 3\%$ of body mass (Phillips et al. 2003). Birds were recaptured when they returned to the nest following foraging trips and the loggers were recovered. Neither this nor deployment of loggers caused any observed injury, distress, or adverse changes in the birds' behavior.

Wind speed and direction

We obtained wind data (6-hourly zonal and meridional wind speed components at a nominal height of 10 m above sea level) from the European Centre for Medium-Range Weather Forecasts on a Gaussian N80 grid (resolution at 54° S, 125×75 km). For periods before March 2002, wind data came from the ERA40 reanalysis data set; for subsequent periods, operational model data were used. To ensure equivalency, operational model data were resampled at the same spatial resolution as the ERA40 data set. We then identified the data subset nearest in time to each tracking location and calculated wind speed (V_{w10}) and direction (θ_w) at that location by interpolation between spatially adjacent points. Wind speeds were reduced to a reference height h_{ref} of 5 m above sea level (i.e., the middle of the range of albatross flight heights typically observed in the field; Pennycuik 1982) using a logarithmic model of wind gradient and assuming a scale height h_0 of 0.03 m (Pennycuik 1982, Sachs 2005):

$$V_{w5} = \frac{V_{w10} (\ln 5 - \ln h_0)}{\ln 10 - \ln h_0}. \quad (1)$$

The flight direction relative to the wind $\Delta\theta$ (i.e., the absolute difference between flight direction θ_f and wind direction θ_w , where $0^\circ \leq \theta_f \leq 180^\circ$) was then calculated and the wind speed component in the direction of flight

(V_{wf}) was calculated as

$$V_{wf} = V_{w5} \cos \Delta\theta. \quad (2)$$

For each section of track analyzed, we calculated the mean wind speed component \bar{V}_{wf} as the average of V_{wf} at all intermediate locations. In addition, we quantified seasonal changes in mean wind speed in the study period and area. For each species, we defined the study area as that bounded by the maximum and minimum latitudes and longitudes reached by tracked birds during the whole breeding season. We then obtained wind speed measurements once every 6 h across this area (reduced to $h_{ref} = 5$ m) as previously described. Finally, we calculated the mean wind speed within the study area during each breeding stage (incubation, brood-guard, and post-brood).

Trip stage

We categorized tracking locations as having been recorded during the outward, middle, or inward stage of foraging trips. Although central-place foraging trips are often regarded as divisible in this way (Orlans and Pearson 1979), in albatrosses the distinction between commuting and foraging varies considerably with species and breeding stage (Weimerskirch et al. 1997b; British Antarctic Survey [BAS], unpublished data). Furthermore, at the individual level it is difficult to objectively identify the transition between such behaviors (BAS, unpublished data). Rather than adopting an arbitrary division on a case-by-case basis, we determined the stage of trips at which these transitions typically occur at the population level (see Appendix B). In short, for each tracking location we calculated the distance from the colony as a proportion of the maximum distance reached during that trip (d_{col}/d_{max}) and the time elapsed as a proportion of the total trip time (t/t_{max}). The rate of change d_{col}/d_{max} with t/t_{max} is a measure of the rate at which birds move relative to the colony. Hence, by graphically examining the variance of d_{col}/d_{max} with t/t_{max} we were able to identify the value of t/t_{max} at which the birds typically ceased commuting rapidly away from the colony and that at which they began commuting rapidly back again. Locations lying between these two values were categorized as the middle stage, and the remainder as the outward or return stages, as appropriate.

Diel and lunar period

Tracking locations were categorized as day or night, night being defined as the period in which the sun was six degrees or more below the horizon (Phillips et al. 2005). Sections of track bounded by pairs of locations (hereafter referred to as L_i and L_{i+n}) were then categorized as daytime, if locations L_i to L_{i+n} were all recorded during the day; nighttime if all were recorded in the night or crepuscular otherwise. We also determined m , the proportion of the moon's disk illuminated at midnight on the day that L_i to L_{i+n} were recorded

using tables supplied by the U.S. Naval Observatory Astrological Applications Department (*available online*).⁶ Where there were sufficient data, nighttime pairs of locations were further subdivided into nights with $m > 0.5$ and those with $m < 0.5$.

Selection of location data

In order to calculate albatross ground speeds (V_g) between pairs of tracking locations, we selected a subset of the location data using the following criteria.

Distance traveled (PTT locations only).—Because PTT location quality decreases as ground speed increases, data sets from fast-moving species such as albatrosses tend to include very few high-quality locations (Weimerskirch et al. 1992); for PTT quality issues, see ARGOS (*available online*).⁷ Errors associated with these locations compromise estimates of speed, unless the distance between locations is sufficiently large. To select tracking locations from comparatively fast-moving albatrosses, we extended the approach of Hays et al. (2001), who used computer simulations to define minimum distance between PTT locations required to reliably estimate the speed of green turtles (*Chelonia midas*). Following an initial sensitivity analysis, we defined the minimum distance d_{sep} between two locations as that which would result in 95% of individual speed estimates lying within $\pm 10\%$ of the true ground speed (cf. Hays et al. 2001). In this way we estimated d_{sep} between all possible pairs of ARGOS location classes (see Appendix C).

Track straightness.—Changes in flight direction of albatrosses occur at smaller time scales (seconds to minutes) than typical PTT tracking intervals (hours). Hence, a bird's true track tends to be longer than the sum of straight-line distances between tracking locations. Values of V_g estimated from tracking data are thus lower than instantaneous V_g , with the discrepancy increasing the more that the bird's track deviates from a straight line. In order to select only relatively direct sections of track, we calculated the straightness index (s) between L_i and L_{i+n} by dividing the great-circle distance between these two locations by the sum of the great-circle distances between consecutive locations along the intervening sections of track (Batschelet 1981, Hays et al. 2001).

Proportion of time on the water.—For those birds equipped with wet-dry loggers, we used immersion data to estimate the proportion of time (p_w) spent on the water between pairs of tracking locations L_i and L_{i+n} .

Statistical tests and models

Unless otherwise stated, statistical methods followed Crawley (2007) and all statistical tests and models were implemented using R statistical software (R Development Core Team 2005). We modeled inter- and

intraspecific variations in ground speed V_g in response to wind speed component V_{wf} , and so on, using linear mixed-effects (LMEs) models fitted using maximum likelihood (Pinheiro and Bates 2000), implemented with the nlme package (Pinheiro et al. 2005). Because multiple pairs of locations were used from some birds, we included individual bird in all models as a random effect. Serial autocorrelation was modeled using a first-order continuous autoregressive structure. We proceeded with backward selection from maximal models (which included all possible interactions and, where relevant, quadratic terms to investigate the possibility of curvature) using the Akaike Information Criterion to compare models. Using the same technique, we tested for differences in wind speeds V_{w5} experienced by albatrosses. Similarly, we tested for differences in relative flight direction $\Delta\theta$ using mixed-effects generalized linear models (GLMMs) implemented with the lme4 package in R (Bates et al. 2008). Fixed-effects parameters are quoted with their estimated 95% CIs, which in a number of cases, where the response variable was square-root or double-square-root transformed to reduce heteroscedasticity, are asymmetrical. Unless otherwise stated, data are presented as means \pm SE. Details of data selection and modeling for each analysis are as follows.

Ground speed in sustained, direct flight vs. size and wind component in the direction of flight (model I).—To test the hypotheses that larger species and sexes of albatrosses fly faster than smaller ones and that ground speed V_g is proportional to the wind speed component in the direction of flight V_{wf} , we calculated V_g for periods in which birds undertook sustained, direct bouts of flight. We selected pairs of locations using the following criteria. In order to compare only commuting periods of flight, PTT locations were retained if they were separated by distances $> d_{min}$. Because errors associated with GPS locations are small (< 10 m; Fukuda et al. 2004, Awkerman et al. 2005) all GPS data were retained at this stage. Few pairs of locations with 0, 1, or 2 intervening locations met the PTT selection criterion, so the analysis was restricted to pairs of locations separated by three intervening locations (i.e., L_i and L_{i+4}). From these data we selected locations with contemporaneous immersion data. In each species, the proportion of time (p_w) spent on the water between pairs of L_i and L_{i+4} had a bimodal distribution, with modes at 0.1 and 0.9. Initial analysis indicated that pairs of locations between which the birds spent $> 10\%$ of their time on the water resulted in highly variable estimates of ground speed. Hence, we retained data where $p_w < 0.1$. Next, we selected only pairs of locations with a straightness index (s) between locations of $s > 0.8$. Although this ensured that we selected bouts of flight that were relatively direct at the scale of hours and hundreds of kilometers, at smaller scales the tortuosity of albatross tracks during foraging varies between species (Pinaud and Weimerskirch 2007). Hence, for greater comparability between taxa we finally

⁶ (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>)

⁷ (<http://www.argos-system.org/>)

retained only pairs of locations drawn from the outward and inward parts of foraging trips, assuming that these were representative of commuting flight in all species.

Following data selection, we estimated the time in flight (t_f) between L_i and L_{i+4} by multiplying Δt , (the time interval between L_i and L_{i+4}) by $1 - p_w$. We then calculated ground speed by dividing the great circle distance between L_i and L_{i+4} by t_f . No correction was made for track straightness, as it was not consistently clear from the data whether deviations from straightness were real or related to location error. We then compared various models of V_g in response to the fixed effects of V_{wf} , trip stage (outward vs. return trips) and size group (defined by species and sex), selecting the most parsimonious. The basic fixed-effects model took the following form:

$$V_g = \alpha + \beta V_{wf}. \quad (3)$$

We also considered Δt as a candidate covariate, to correct, if necessary, for potential bias in V_g arising from interspecific differences in the temporal resolution of the tracking data.

Ground speed during sustained, direct flight vs. wind component in the direction of flight, sex, breeding stage, trip stage, Δt , and diel and lunar periods (models IIa–IIId).—We next examined each species in more detail, considered potential effects of different covariates, and tested the hypotheses (1) that V_g is higher in males and (2) that $V_g \approx V_{wf}$. We calculated ground speed as described for model I, with the following differences. First, because we did not wish to make interspecific comparisons, we were able to treat the GPS (Wandering Albatross) data somewhat differently than the PTT data in order to increase sample size and the accuracy of our estimates of V_g . Hence, for Wandering Albatrosses we used adjacent locations (i.e., L_i and L_{i+1}) to calculate V_g and locations to either side of these (L_{i-1} and L_{i+2}) to calculate the straightness index s (s must be calculated over three or more locations). In addition, for all species we increased sample size further by including locations from throughout foraging trips (outward, middle, and inward stages) in this analysis. We then modeled V_g in response to V_{wf} , sex, breeding stage (incubation/brood-guard/post-brood), trip stage, Δt , and diel and, where possible, lunar period.

Ground speed during sustained flight vs. sex, breeding stage, and trip stage (models IIIa–IIIId).—We tested for significant differences in observed ground speeds between sexes, breeding stages, and trip stages as follows. To retain a large sample size, we calculated V_g between adjacent locations L_i and L_{i+1} , selecting pairs of locations if the bird had been in flight >90% of the time between them. Ground speeds were corrected, where necessary, for time spent in flight, and both direct and indirect bouts of flight were retained (i.e., no straightness criterion was imposed). We then modeled V_g in response to sex, breeding stage, and trip stage.

Wind was not considered as a candidate covariate in these models.

Wind speed vs. sex, breeding stage, and trip stage (models IVa–IVd).—We compared wind speeds experienced by foraging albatrosses by modeling V_{w5} at all tracking locations, in response to sex, breeding stage, and trip stage. We also compared wind direction, averaged by individual, between species, sexes, breeding stages, and trip stages using circular ANOVA models (Mardia and Jupp 2000), implemented with the “circular” package in R (Lund and Agostinelli 2007). Circular mean wind directions are quoted with ρ , their mean resultant length.

Flight direction relative to wind direction during sustained flight vs. sex, breeding stage, and trip stage (models Va–Vd).—We calculated $\Delta\theta$ for pairs of adjacent locations L_i and L_{i+1} between which birds were in flight >90% of the time. For each stage within individual foraging trips, we then calculated median $\Delta\theta$. We modeled the response of this variable to sex, trip stage, and breeding stage using mixed-effects generalized linear models implemented with the lme4 package in R (Bates et al. 2008). Because median $\Delta\theta$ is bounded above and below, we rescaled it from 0 to 1 and employed a binomial error structure with the logit link function. Although this approach allows multilevel comparisons to be made while avoiding pseudoreplication, it is rather conservative. Therefore, we also tested the hypothesis that $\Delta\theta$ differed between outward and inward phases of foraging trips by comparing median outward and inward $\Delta\theta$ values using Wilcoxon matched-pairs tests. Similarly, we tested for between-species differences in $\Delta\theta$ during the middle stages of trips with a Kruskal-Wallis test, making the assumption in both cases that individual foraging trips were independent.

Theoretical ground speed predictions

A consideration of the morphology of a gliding bird allows its theoretical optimum airspeed in different circumstances to be calculated. The minimum sink speed V_{ms} occurs when height lost per unit time is minimized, whereas height lost per unit distance is minimized at a higher airspeed, the best glide speed V_{bg} (Pennycuik 1989). When V_{wf} is zero, a bird’s ground speed V_g is equal to its airspeed, and can thus be predicted when this condition is met. However, such predictions of V_g relate to instantaneous speeds and are likely to be greater than ground speeds recorded over larger spatial scales (as in this study). For this reason, we calculated the theoretical differences between group (species and sex) ground speeds and compared these (rather than absolute values) with differences in V_g given by our empirical models (i.e., differences in the value of the intercepts, α). Theoretical airspeeds (V_{bg} and V_{ms}) of each species and sex were predicted following Pennycuik (1989), using the computer program Flight Version 1.17 (Pennycuik 2006) at $h_{ref} = 5$ m. Morphometrics of Black-browed, Gray-headed, and Light-mantled Sooty

TABLE 1. Model I, linear mixed-effects model of ground speed V_g in response to wind speed component in the direction of flight V_{wf} of four species of albatross.

Albatross species	Sex	Intercept, α			Slope, β		
		Estimate \pm 95% CI (m/s)	t	P	Estimate \pm 95% CI (m/s)	t	P
Black-browed	F	9.59 \pm 1.83	10.140	<0.001	0.70 \pm 0.22	6.109	<0.001
	M	12.50 \pm 2.40	2.380	0.020	0.58 \pm 0.27	-0.908	0.365
Wandering	F	10.01 \pm 2.09	0.402	0.689	0.45 \pm 0.26	-1.856	0.064
	M	9.76 \pm 2.08	0.164	0.870	0.36 \pm 0.26	-2.625	0.009
Gray-headed	F	10.63 \pm 2.35	0.866	0.389	0.22 \pm 0.33	-2.810	0.005
	M	10.41 \pm 2.20	0.737	0.464	0.45 \pm 0.29	-1.738	0.083
Light-mantled Sooty	U	10.66 \pm 2.62	0.807	0.422	0.50 \pm 0.30	-1.368	0.172

Notes: Total sample sizes are 78 individual birds and 423 pair locations (tracking interval 10.27 ± 0.15 h, mean \pm SD). Sexes are F, female; M, male; U, unsexed. Estimated $df = 71$ for α , all species and sexes except for female Black-browed Albatrosses ($df = 338$). Estimated $df = 338$ for β , all species and sexes. For female Black-browed Albatrosses, P refers to the overall significance of α and β , while for all other species and sexes, P refers to the difference between these and group parameters.

Albatrosses taken at their breeding colonies on Bird Island (Phillips et al. 2004; BAS, unpublished data) were entered into the program. Insufficient measurements of Wandering Albatrosses were available from this colony so we used published values for this species at Crozet (Shaffer et al. 2001). The mass of instruments had a negligible effect on predicted parameters and was not considered further in our calculations.

RESULTS

Empirical and theoretical models of ground speed

Examination of the variance of d_{col}/d_{max} with t/t_{max} showed that, in all species, foraging trips were characterized by an initial rapid movement away from the colony, which we classified as the outward stage. Then followed a period of slower and more variable (positive and negative) movement with respect to the colony (middle stage), followed by a period of rapid movement back towards the colony (return stage). The division between these stages occurred, on average, when 20% and 81% of the total trip time had elapsed (Appendix B).

For pairs of PTT locations of the same location class, d_{sep} was directly proportional to the location error σ ($d_{sep} = 28.19\sigma - 0.21$, $R^2 = 1.0$, $P < 0.001$; Appendix C). In total, 9% of pairs of PTT locations (L_i to L_{i+4}) were separated by distances $> d_{sep}$. This, along with the other selection criteria, meant that 4% of pairs of PTT locations and 8% of pairs of GPS locations were retained for analysis in model I. Observed ground speeds (V_g) between these locations ranged from a minimum of 2.2 m/s for a Wandering Albatross to a maximum of 26.8 m/s for a Black-browed Albatross. Mean V_g was very similar across species and ranged from 10.4 ± 0.2 m/s for Wandering Albatrosses to 13.4 ± 0.3 m/s for Black-browed Albatrosses (mean V_g of Gray-headed and Light-mantled Sooty Albatrosses was 11.6 ± 0.3 and 12.4 ± 0.3 m/s, respectively).

Estimated ground speed was negatively correlated with Δt in both the PTT and GPS data (Spearman rank correlation: for PTT data, $r_s = -0.36$, $N = 231$ locations, $P < 0.001$; for GPS data, $r_s = -0.18$, $N = 192$ locations, $P = 0.010$). However, Δt was not retained as an

explanatory variable in any of the models describing V_g . In model I both V_{wf} and size group were retained as explanatory variables (Table 1). Trip stage was rejected, however, indicating that there were no significant differences in V_g in response to V_{wf} (measured during direct and uninterrupted bouts of flight) between outward vs. inward stages of foraging trips. As expected, V_g was serially autocorrelated in this and all of the other LME models that we will describe (the autocorrelation parameter ϕ ranged from 0.42 to 0.90). The intercept α (i.e., V_g in zero relative wind; Fig. 1) was greatest for male Black-browed Albatrosses (12.5 m/s) and lowest for male Wandering Albatrosses (9.8 m/s). In Black-browed Albatrosses, α was significantly greater for males than females (9.6 m/s) but significant intersexual differences were not evident in other species.

As expected, theoretical values of V_{ms} and V_{bg} (Table 2) were proportional to the square root of wing loading ($V_{ms} = 0.91(\text{wing loading})^{0.5}$, $R^2 = 0.9$, $P < 0.001$; $V_{bg} = 4.5 + 0.84(\text{wing loading})^{0.5}$, $R^2 = 0.9$, $P < 0.05$). In the smaller species (*Thalassarche* and *Phoebastria*), absolute

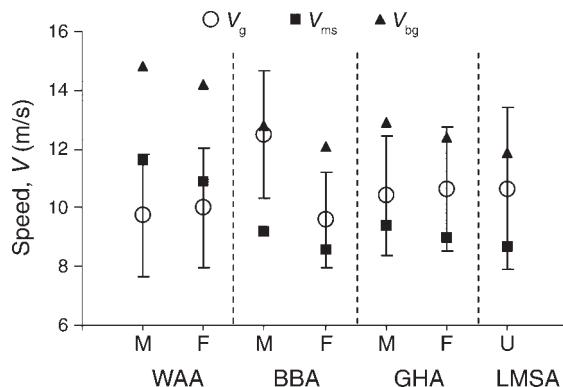


FIG. 1. Ground speed, V_g (mean and 95% CI), in zero relative wind as predicted by model I, theoretical minimum sink speeds (V_{ms}), and best glide speeds (V_{bg}) of male (M) and female (F) Wandering Albatrosses (WAA), Black-browed Albatrosses (BBA), Gray-headed Albatrosses (GHA), and unsexed (U) Light-mantled Sooty Albatrosses (LMSA).

TABLE 2. Wing loading (mean \pm SD), theoretical minimum sink speed (V_{ms}), and best glide speed (V_{bg}) of four species of albatrosses.

Albatross species	Sex	n	Wing loading (N/m ²) [†]	V_{ms} (m/s)	V_{bg} [‡] (m/s)
Wandering	M	20	148 \pm 10	11.6	14.8
	F	16	132 \pm 11	10.9	14.2
Black-browed	M	18	92 \pm 5	9.2	12.8
	F	14	82 \pm 4	8.6	12.1
Gray-headed	M	19	97 \pm 7	9.4	12.9
	F	13	89 \pm 6	9.0	12.4
Light-mantled Sooty	U	10	85 \pm 8	8.7	11.9

Note: Sexes are: F, female; M, male; U, unsexed. Sample size (n) is the number of individuals.

[†] Sources: Phillips et al. (2004), Shaffer et al. (2001); British Antarctic Survey [BAS], unpublished data.

[‡] Calculated using Flight Version 1.17 (Pennycuik 2006).

values of α lay between V_{ms} and V_{bg} but relative magnitudes differed from those predicted (in male Black-browed Albatrosses α was ~ 2 m/s, greater than expected in comparison to the other species or sexes, in absolute terms being $\approx V_{bg}$). The values of α for Wandering Albatrosses were ~ 2 m/s lower than expected, their absolute values lying below V_{ms} . In all groups there was a strong linear relationship between V_g and V_{wf} . There was considerable variation in the effect of V_{wf} , however, as indicated by the slope parameter β . This was greatest for female Black-browed Albatrosses ($\beta = 0.70$) and lowest for female Gray-headed Albatrosses ($\beta = 0.22$).

The less exclusive criteria used to select data for the species-specific models of ground speed in response to V_{wf} and other covariates (IIa–IIb) resulted in retention of 7% of PTT and 11% of GPS data. This, together with

the larger number of covariates considered, produced better model performance (95% CIs on parameter estimates in models IIa–IIc were approximately half those in model I; Table 3). Parameter estimates from model IIc (Light-mantled Sooty Albatrosses) had relatively large confidence intervals, however, and should be treated with caution. Nevertheless, the ground speed of Light-mantled Sooty Albatrosses fitted the general trend described for the other species. In all species there was a strong linear relationship between V_g and V_{wf} , and within species this relationship did not differ significantly between sexes. The rate of change of V_g with V_{wf} was greatest in Wandering Albatrosses ($\beta = 0.59$) and least in Gray-headed Albatrosses ($\beta = 0.33$). When variability due to V_{wf} is accounted for, models IIa–IIc show that male Wandering, Black-browed, and Gray-headed Albatrosses all flew significantly faster than females (the sex of Light-mantled Sooty Albatrosses was not known). Model IIa (Wandering Albatrosses) was the best-performing model (based on the width of 95% CIs) and suggests that V_g of males (12.4 m/s) is 1.0 m/s greater than females (Fig. 2). This difference is slightly larger than the theoretical sexual difference in V_{ms} and V_{bg} (0.7 and 0.6 m/s) predicted using Flight Version 1.17 (cf. Tables 2 and 3). Models IIb and IIc show that in the two *Thalassarche* spp. the V_g of males was 1.4 m/s greater than that of females (male Black-browed Albatross daytime $V_g = 12.0$ m/s, male Gray-headed Albatross $V_g = 10.8$ m/s). Again, these were slightly larger than theoretical sexual difference in V_{ms} (0.6 and 0.7 m/s, respectively) and V_{bg} (0.4 and 0.5 m/s, respectively).

TABLE 3. Models IIa–IIc, linear mixed-effects models of ground speed V_g (m/s) in response to wind speed component in the direction of flight V_{wf} (m/s) of four species of albatrosses during direct, sustained bouts of flight.

Model and covariate/level	Estimate \pm 95% CI	df [†]	t	P [‡]
IIa) Wandering Albatrosses (43 birds, 476 locations, interval 1.47 \pm 0.06 h)				
V_{wf} (β)	0.59 \pm 0.06	330	17.783	<0.001
Female, outward trip (group α)	11.40 \pm 0.62	430	36.232	<0.001
Male	+0.98 \pm 0.65	41	3.046	0.004
Middle of trip	-0.69 \pm 0.68	430	-1.967	0.050
Return trip	-0.10 \pm 0.79	430	-0.250	0.803
IIb) Black-browed Albatrosses (12 birds, 199 locations, interval 10.49 \pm 0.12 h)				
V_{wf} (β)	0.53 \pm 0.10	185	9.908	<0.001
Female, night (group α)	9.69 \pm 1.06	185	18.008	<0.001
Male	+1.42 \pm 1.29	10	2.454	0.034
Day	+0.86 \pm 0.74	185	2.282	0.024
IIc) Gray-headed Albatrosses (30 birds, 135 locations, interval 12.16 \pm 0.13 h)				
V_{wf} (β)	0.33 \pm 0.11	14	5.674	<0.001
Female (group α)	9.43 \pm 0.98	14	18.870	<0.001
Male	+1.37 \pm 1.21	28	2.286	0.030
IIc) Light-mantled Sooty Albatrosses (3 birds, 127 locations, interval 11.62 \pm 0.12 h)				
V_{wf} (β)	0.43 \pm 0.14	123	5.913	<0.001
Unsexed (group α)	9.81 \pm 1.81	123	10.669	<0.001

Note: Tracking intervals are given as mean \pm SD.

[†] Estimated degrees of freedom.

[‡] P refers to group α and to differences between this and α for the remaining covariates/levels.

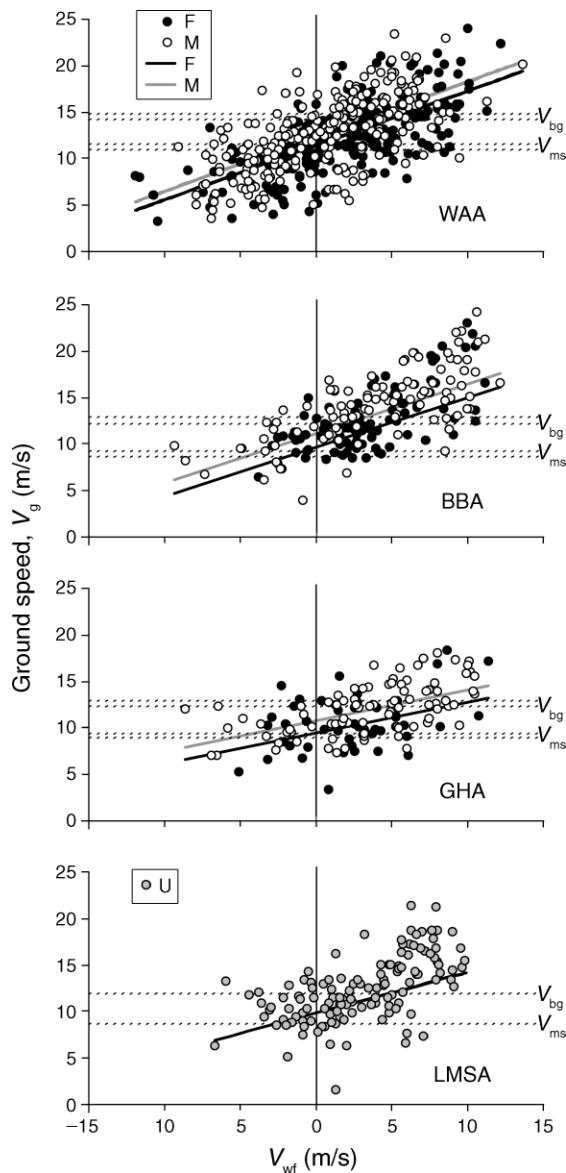


FIG. 2. Linear mixed-effects models of ground speed (V_g ; circles and heavy lines for females [F], males [M], and unsexed birds [U]) in response to the wind speed component in the direction of flight (V_{wf}) for Wandering Albatrosses tracked with GPS tags (WAA, model IIa); Black-browed Albatrosses tracked with PTTs (BBA, model IIb); Gray-headed Albatrosses tracked with PTTs (GHA, model IIc); and unsexed Light-mantled Sooty Albatrosses tracked with PTTs (LMSA, model IIId). Also shown are theoretical best glide speeds (V_{bg}) and minimum sink speeds (V_{ms}) of males (upper dashed line) and females (lower dashed line); both sexes are combined for Light-mantled Sooty Albatrosses.

Of the pairs of locations selected for analysis in model IIa (Wandering Albatrosses), 23% were from the nighttime. The proportion of the moon's disk illuminated (m) when these pairs of locations were recorded was no different than that expected by chance ($\chi^2 = 4.267$, $df = 3$, $P = 0.234$). Of the nighttime pairs of

locations, 47% were recorded when $m < 0.5$, and 25% were recorded when $m < 0.25$. This, together with the fact that diel/lunar period was rejected as an explanatory variable in model IIa, indicates that Wandering Albatrosses were able to sustain direct, uninterrupted flight during darkness. For the other species, few pairs of nighttime locations met the selection criteria (4%, 1%, and 6% for Black-browed, Gray-headed, and Light-mantled Sooty Albatrosses, respectively). Furthermore, in all species the majority of these pairs of locations (67%), and significantly more than would be expected by chance alone ($\chi^2 = 15.527$, $df = 3$, $P = 0.001$), were recorded on nights with bright moonlight ($m > 0.75$). As there were insufficient data in the nighttime categories for the purposes of models IIb–IIId, we reclassified pairs of locations as being nighttime if they were recorded wholly or partly in the dark, and the remainder as daytime. Diel period was rejected as an explanatory variable for Gray-headed and Light-mantled Sooty Albatrosses, but was retained for Black-browed Albatrosses (model IIb). Daytime V_g was 0.9 m/s faster than nighttime V_g in Black-browed Albatrosses.

Breeding stage was rejected as an explanatory variable in all models. Similarly, trip stage was rejected in all but model IIa, which showed that V_g in Wandering Albatross was slightly lower (0.69 ± 0.68 m/s) during the middle than the outward stages of foraging trips. This effect, however, was only marginally significant ($P = 0.050$).

Models IIIa, IIIb, and IIIc (Table 4) show that when V_{wf} was not considered, ground speeds of Wandering, Black-browed, and Light-mantled Sooty Albatrosses (estimated for sustained flight between two consecutive locations) were significantly faster during the return than during the outward stages of trips (1.0, 3.4, and 1.4 m/s faster, respectively). In addition the V_g of Black-

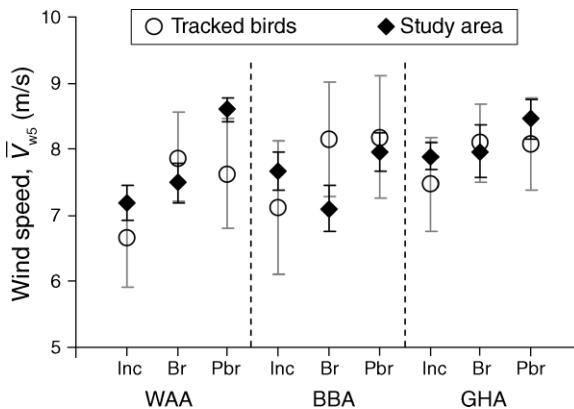


FIG. 3. Wind speed at 5 m above sea level (\bar{V}_{w5}) experienced by albatrosses tracked from Bird Island, South Georgia, and wind speed averaged across the area traversed by each species during different stages of the breeding season (mean and 95% CI). Abbreviations are: WAA, Wandering Albatrosses; BBA, Black-browed Albatrosses; GHA, Gray-headed Albatrosses; Inc, incubation; Br, brood-guard; Pbr, post-brood.

TABLE 4. Models IIIa–IIIId, linear mixed-effects model of ground speeds V_g (m/s) of four species of albatrosses, during both direct and indirect flight.

Model and covariate/level	V_g estimate (95% CI) (m/s)	df†	t	$P‡$
IIIa) Wandering Albatrosses (46 birds, 1651 locations, interval 1.21 ± 0.04 h)				
Outward trip, brood-guard (group α)	8.7 (7.72, 9.73)	1594	33.858	<0.001
Middle of trip	-0.23 (-0.83, 0.39)	1594	-0.738	0.460
Return trip	+1.02 (0.26, 1.81)	1594	2.662	0.008
Incubation	+2.56 (1.06, 4.16)	43	3.541	0.001
Post-brood	+0.78 (-0.48, 2.12)	43	1.23	0.225
IIIb) Black-browed Albatrosses (12 birds, 2728 locations, interval 2.00 ± 0.06 h)				
Outward trip (group α)	9.09 (8.53, 9.67)	2496	124.696	<0.001
Middle of trip	-1.2 (-1.61, -0.76)	2496	-5.187	<0.001
Return trip	+3.39 (2.60, 4.23)	2496	9.143	<0.001
IIIc) Gray-headed Albatrosses (34 birds, 1112 locations, interval 2.52 ± 0.06 h)				
Outward trip, brood-guard (group α)	12.27 (11.15, 13.44)	1064	42.1	<0.001
Middle of trip	-4.19 (-5.00, -3.34)	1064	-8.833	<0.001
Return trip	-1.10 (-2.22, 0.08)	1064	-1.833	0.067
Incubation	-2.19 (-3.18, -1.15)	11	-4.503	0.001
IIIId) Light-mantled Sooty Albatrosses (3 birds, 641 locations, interval 2.33 ± 0.06 h)				
Outward trip (group α)	9.31 (8.23, 10.45)	616	32.707	<0.001
Middle of trip	-0.43 (-1.40, 0.59)	616	-0.840	0.401
Return trip	+1.41 (0.13, 2.77)	616	2.158	0.031

Note: Tracking intervals are given as mean \pm SD.

† Estimated degrees of freedom.

‡ P refers to group α and to differences between this and α for the remaining covariates/levels.

browed Albatrosses was ~ 1.2 m/s slower during the middle than outward stages of foraging trips. Ground speeds in the middle stages were also considerably (4.2 m/s) slower in Gray-headed Albatrosses (model IIIc), but there was no significant difference between outward and inward stages in this species. Sexual differences in V_g could not be detected when the data were treated in this way (sex was not retained as an explanatory variable in any of these models). However, breeding stage was retained for Wandering and Gray-headed Albatrosses. In the former species, birds during the incubation stage flew some 2.6 m/s faster than those during brood-guard. In contrast, Gray-headed Albatrosses during the incubation stage flew 2.2 m/s slower than those during brood-guard.

Wind conditions experienced during foraging flights

Birds of all species and sexes experienced similar wind conditions while foraging. Wind speeds experienced by individuals ranged from 0.1 to 20.6 m/s, with an overall mean of 7.7 ± 3.1 m/s. There were no significant differences between mean wind speeds experienced by individual Wandering (7.7 ± 1.4 m/s), Black-browed (7.8 ± 0.9 m/s), Gray-headed (7.6 ± 1.2 m/s), and Light-mantled Sooty Albatrosses (6.6 ± 0.5 m/s) (ANOVA, $F_{3,145} = 1.67$, $P = 0.176$). For all species sexed, gender was rejected as an explanatory variable in models IVa–IVc, indicating that male and female birds experienced comparable wind speeds throughout the breeding season (Table 5). Trip stage was also rejected in models IVa–IVd, demonstrating that wind speed did not differ

TABLE 5. Models IVa–IVc, linear mixed-effects model of wind speed V_{w5} (m/s) experienced by three species of albatrosses.

Model and covariate/level	V_{w5} estimate (95% CI) (m/s)	df†	t	$P‡$
IVa) Wandering Albatrosses (43 birds, 2174 locations)				
Brood-guard (group α)	7.87 (7.21, 8.56)	2125	45.660	<0.001
Incubation	6.67 (5.92, 7.46)	46	-3.018	0.004
Post-brood	7.61 (6.80, 8.46)	46	-0.631	0.531
IVb) Black-browed Albatrosses (50 birds, 1750 locations)				
Brood-guard (group α)	8.16 (7.29, 9.02)	1700	18.593	<0.001
Incubation	7.12 (6.10, 8.13)	47	-2.062	0.045
Post-brood	8.18 (7.25, 9.10)	47	0.049	0.961
IVc) Gray-headed Albatrosses (45 birds, 1226 locations)				
Brood-guard (group α)	8.10 (7.51, 8.68)	1085	27.043	<0.001
Incubation	7.47 (6.76, 8.18)	95	-1.749	0.084
Post-brood	8.07 (7.37, 8.78)	43	-0.065	0.949

† Estimated degrees of freedom.

‡ P refers to group α and to differences between this and α for the remaining covariates/levels.

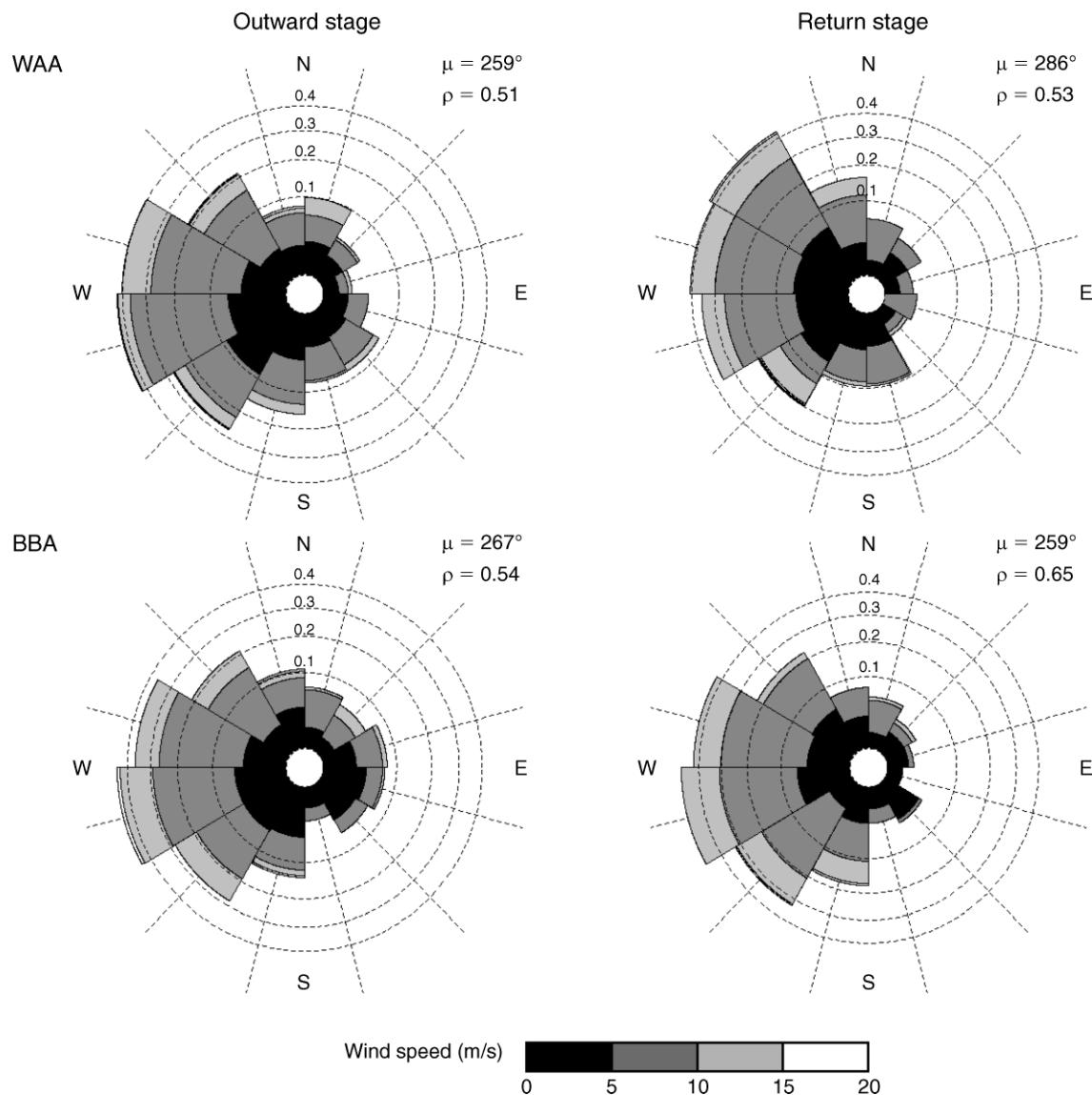


FIG. 4. Wind speed and direction experienced by albatrosses tracked from Bird Island, South Georgia, during outward and return portions of foraging trips. Species are: WAA, Wandering Albatrosses; BBA, Black-browed Albatrosses; GHA, Gray-headed Albatrosses; LMSA, Light-mantled Sooty Albatrosses. Circles indicate the percentage of winds from a given direction, and shading indicates the proportion of wind speeds of a given magnitude: μ is mean wind direction and ρ is mean resultant length, a measure of the spread of directional data, varying from 0 (dispersed) to 1 (unidirectional).

significantly between the outward, middle, and inward stages of foraging trips. In contrast, breeding stage was retained in all models for the species from which we collected multistage tracking data (Wandering, Black-browed, and Gray-headed Albatrosses). In each species, wind speeds did not differ between brood-guard and post-brood stages, but were ~ 1.2 – 0.6 m/s lower during incubation (although this difference was not significant in Gray-headed Albatrosses; Fig. 3). Mean wind speeds experienced by albatrosses during each breeding stage were generally similar to those calculated across the study area for corresponding periods. This suggests that

differences in wind speeds experienced between stages were due to seasonal changes in the intensity of the wind, rather than to habitat preference.

There was little variability in mean wind directions experienced by birds, with all species predominantly experiencing westerly winds (mean wind direction 270° , $\rho = 0.49$; Fig. 4). In all but one case there were no significant differences in mean wind directions experienced across species, breeding stages, or sex. The exception was Wandering Albatrosses, which experienced winds from significantly more southerly directions during post-brood (253° , $\rho = 0.81$) than during

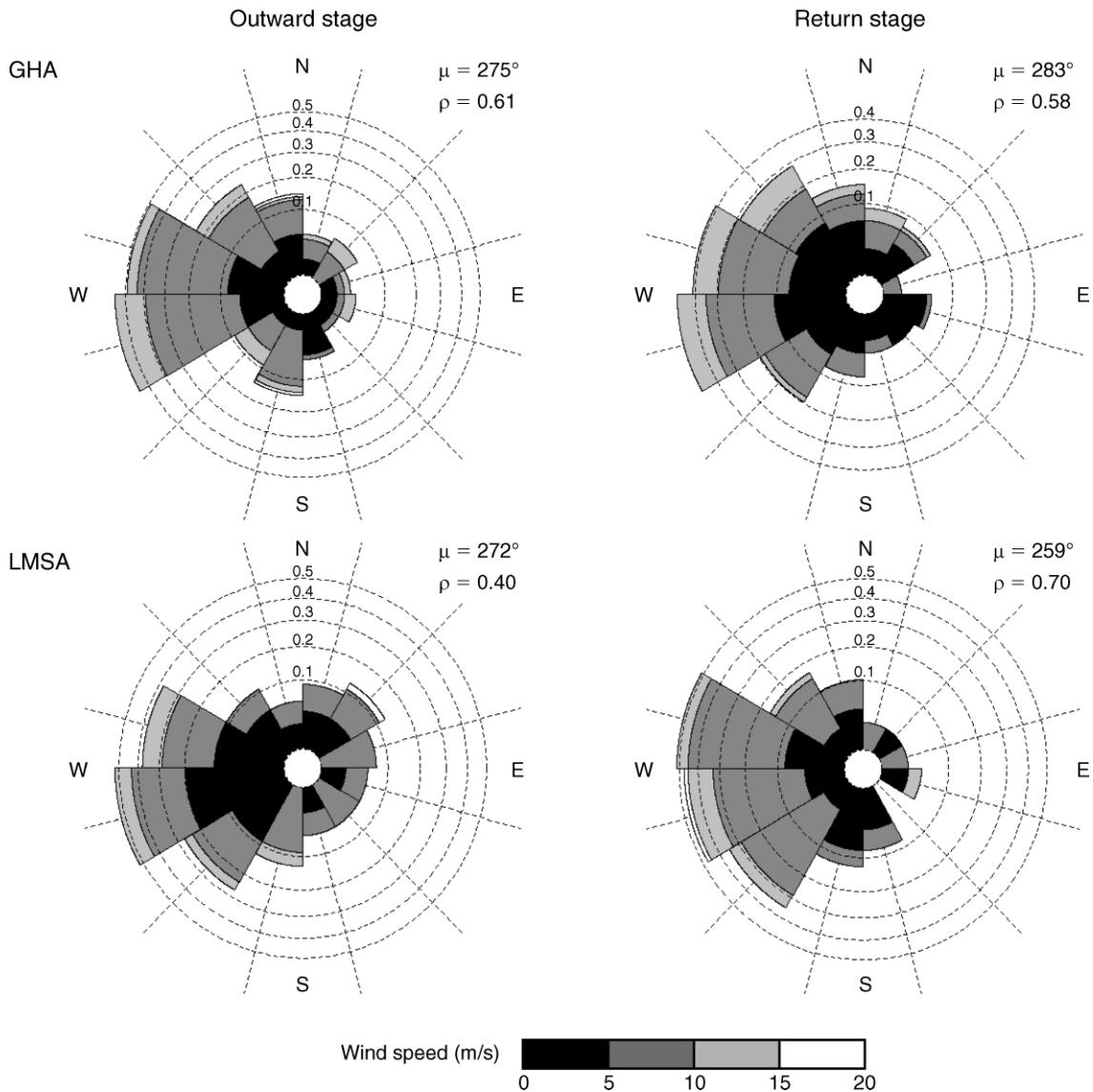


FIG. 4. Continued.

incubation (277° , $\rho = 0.96$) and brood-guard (273° , $\rho = 0.98$) (circular ANOVA, $F_{2,51} = 4.23$, $P = 0.012$). Wind directions did not differ significantly between outward and inward phases of foraging trips.

Flight direction with respect to wind

With some exceptions there was a general tendency for albatrosses to avoid headwind flight and there was no evidence of sexual differences in flight direction relative to wind direction $\Delta\theta$. For Wandering, Gray-headed, and Light-mantled Sooty Albatrosses, the null model (models Va, Vc, and Vd) best described median $\Delta\theta$, indicating that there were no gross differences in relative flight directions between breeding stages and trip stages in these species. Model Vb, however, shows that median $\Delta\theta$ was significantly more downwind during the

return stage of foraging trips made by post-brood Black-browed Albatrosses; i.e., birds often encountered headwinds during the outward stages of foraging trips and tailwinds during the return stages (Table 6). Furthermore, distributions of $\Delta\theta$ show that this trend was evident in all other species and stages considered, except

TABLE 6. Model V_b , generalized linear mixed-effects model of median flight direction relative to wind direction ($\Delta\theta$) of Black-browed Albatross (12 birds, 128 trips).

Covariate/level	Estimate \pm SE†	z	P
Outward trip	0.162 \pm 0.177	0.914	0.361
Middle of trip	-0.102 \pm 0.251	-0.406	0.685
Return trip	-0.915 \pm 0.260	-3.525	<0.001

† $\Delta\theta$ scaled from 0 (downwind) to 1 (upwind) and expressed in logits.

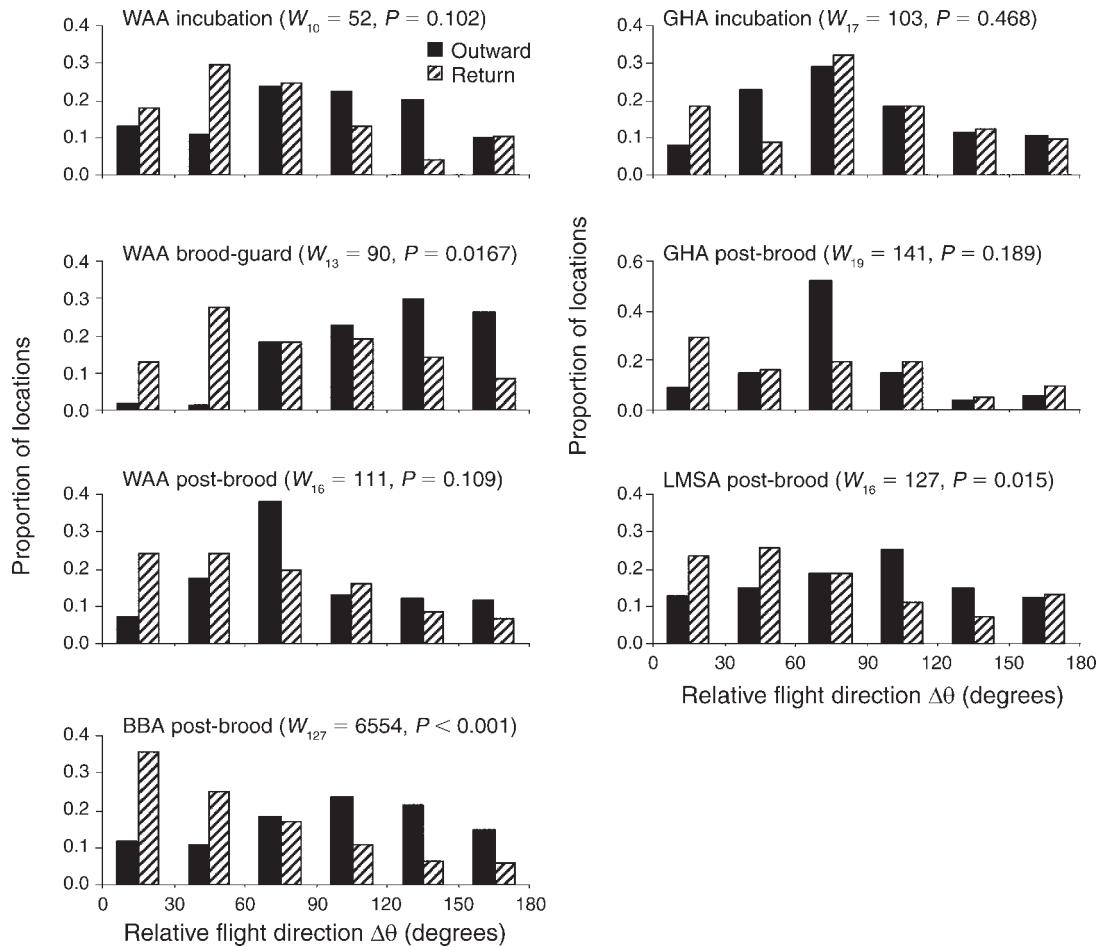


FIG. 5. Distribution of albatross flight directions relative to the wind ($\Delta\theta$) during the outward and return portions of foraging trips. Also shown are Wilcoxon matched-pairs test statistics for outward vs. return $\Delta\theta$. Species are: WAA, Wandering Albatrosses; BBA, Black-browed Albatrosses; GHA, Gray-headed Albatrosses; LMSA, Light-mantled Sooty Albatrosses.

for Gray-headed Albatrosses during incubation. Indeed, Wilcoxon matched-pairs tests confirm that, for individual foraging trips, median $\Delta\theta$ during return stages was significantly more downwind than during outward stages in Wandering Albatrosses during brood-guard, and Black-browed and Light-mantled Sooty Albatrosses during post-brood (Fig. 5). This difference was most marked in the former two species and stages. Relative flight directions during the middle stage of foraging trips were remarkably similar for all species (Kruskal-Wallis $\chi^2_3 = 5.12$, $P = 0.163$), with birds showing a marked tendency to fly across the wind (Fig. 6).

DISCUSSION

We modeled the ground speeds of albatrosses during bouts of direct, sustained flight, over periods of hours. We found that ground speed is a function of the wind component V_{wf} , species, and, where this could be tested, sex. Although female albatrosses had lower ground speeds than males, they did not experience significantly

lower wind speeds. At the scale of hours, albatrosses foraging from South Georgia often encounter headwinds during the outward stages of foraging trips and tailwinds on their return.

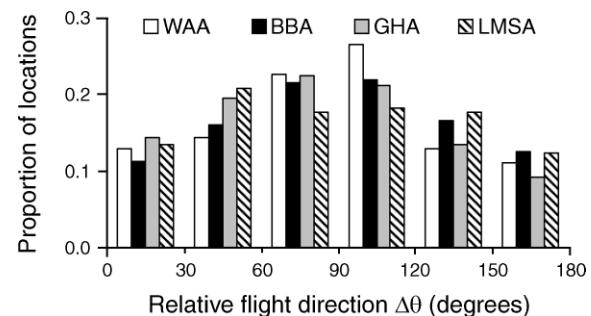


FIG. 6. Distribution of albatross flight directions relative to the wind ($\Delta\theta$) during the middle portions of foraging trips. Species are: WAA, Wandering Albatrosses; BBA, Black-browed Albatrosses; GHA, Gray-headed Albatrosses; LMSA, Light-mantled Sooty Albatrosses.

Selection of tracking locations

Our simulations show that the minimum distances d_{sep} required to obtain accurate estimates of speed using pairs of PTT locations are relatively large. For pairs of locations with equal ARGOS errors, our estimates of d_{sep} were approximately three times those calculated by Hays et al. (2001). This disparity arises for two reasons. First, because there is no consensus on the size of ARGOS errors (Brothers et al. 1998, Hays et al. 2001, Vincent et al. 2002), we adopted the precautionary approach of selecting the largest errors reported in the literature to estimate d_{sep} . Second, whereas Hays et al. (2001) defined d_{sep} as the minimum distance required between two locations to ensure that the *mean* of speeds estimated from a series of pairs of locations lies within $\pm 10\%$ of the true mean speed on 95% of occasions, we defined d_{sep} more stringently as the minimum distance required to ensure that 95% of *all* speed estimates between locations lie within $\pm 10\%$ of the true speed. Therefore, although fewer pairs of PTT locations are retained using our approach, individual speed estimates are more accurate.

Intrinsic and extrinsic factors affecting ground speed

With the exception of model II d (Light-mantled Sooty Albatross), our empirical models of ground speed for each species performed well. In contrast, model I, which considered all species and sexes, performed poorly. Nevertheless, taken together, these models give a good indication of the following intrinsic and extrinsic factors affecting ground speed.

Wind speed component in the direction of flight.—We have shown that ground speeds of albatrosses are proportional to V_{wf} . Pennycuick (1982) reached a similar conclusion after tracking albatrosses optically at a smaller spatial scale. Likewise, other studies have shown V_{g} to be proportional both to $\cos \Delta\theta$ and to \bar{V}_{w5} , the product of which is V_{wf} (Salamolard and Weimerskirch 1993, Spear and Ainley 1997b, Weimerskirch et al. 2000b). In all species, we estimated $\beta < 1$ (Tables 1 and 3). Therefore, ground speed is not simply the product of airspeed and V_{wf} . A possible explanation for this is that the flight height that we assumed ($h_{\text{ref}} = 5$ m) was inappropriate. Although albatrosses periodically perform pull-up maneuvers to heights of 5–10 m during dynamic or gust soaring (Pennycuick 2002), personal observations suggest that they spend most of their time flying very close to the surface of the sea. As wind speed decays exponentially with decreasing height above the sea's surface (Eq. 1), the apparent wind speeds that birds experience may be lower than that at h_{ref} . More accurate data on flight heights would help to resolve this issue. Airspeed optimization (Pennycuick 1978, 1982) and changes in the degree to which flight paths meander with relative flight direction (Alerstam et al. 1993) may also act to modify β . We found no evidence that β differed between sexes, but it did differ between species (Tables 1 and 3). A possible explanation is that the mode of flight

(e.g., defined as the change in flight height throughout the dynamic or gust soaring cycle) varied accordingly. The size of β , and thus the effect of wind on V_{g} , was greatest for Wandering Albatrosses, followed by Black-browed, Light-mantled Sooty, and Gray-headed Albatrosses.

Species.—Interspecific differences in airspeed (i.e., V_{g} in crosswind flight) differed from theoretical predictions based on morphology. Despite their large size and greater wing loading, Wandering Albatrosses had comparatively low ground speeds. This discrepancy may be behavioral in origin rather than due to morphological constraint. By using pairs of locations from the outward and return stages of trips in model I, we assumed that ground speed estimates would pertain to commuting only. This may be a better assumption for the smaller species, such as Black-browed, than for Wandering Albatrosses. The former tend to undertake rapid commuting flights between the colony and discrete, predictable foraging areas, whereas Wandering Albatrosses are thought to search for widely spaced prey over larger areas (Weimerskirch et al. 1997b, Weimerskirch and Guionnet 2002, Catry et al. 2004b). When both direct and indirect flight bouts are considered (models IIIa–IIIb), it can be seen that the V_{g} of Black-browed and Gray-headed Albatrosses decrease significantly during the middle stages of trips (Table 4). This is probably because at fine scales tracks become more tortuous during prey searching (Veit 1999). That such a difference was seen for Wandering Albatrosses suggests less of a marked change in behavior during the middle stages of trips. Optimal foraging theory predicts that gliding birds should fly at airspeeds at, or in excess of, their best glide speed (V_{bg}) when commuting, and at lower speeds (intermediate between V_{bg} and their minimum sink speed V_{ms}) when searching for prey (Pennycuick 1989, Hedenström and Alerstam 1995). Hence the comparatively low speeds estimated for Wandering Albatrosses may be because they were engaged in prey search throughout foraging trips.

Albatross flight paths are convoluted across a range of scales, so estimates of V_{g} tend to decrease with the scale of measurement (Walker et al. 1995). Hence, our estimates of Wandering Albatross V_{g} were ~ 2 m/s higher when calculated between consecutive locations (model IIa) than over five locations (model I). At the scale of minutes and seconds, albatross V_{g} is higher still: ground speeds of Wandering, Black-browed, and Gray-headed Albatrosses measured optically and by radar in zero relative wind were 0.7 to 2.5 m/s faster (Pennycuick 1982, Alerstam et al. 1993) than we estimated with models IIa–IIc, whereas those of Wandering Albatrosses tracked with high-resolution GPS loggers were 2.9 m/s faster (Weimerskirch et al. 2007). Therefore, our estimates of V_{g} at the scale of hours are probably ~ 80 – 94% of instantaneous V_{g} .

Sex.—In accordance with theoretical predications, the V_{g} of males in zero relative winds ($V_{\text{wc}} = 0$) were

significantly higher than those of females. Although this result is not entirely unprecedented (mean V_g of Red-footed Boobies *Sula sula*, which exhibit reverse sexual dimorphism but proceed largely by flapping flight, is higher in females; Weimerskirch et al. 2006), to our knowledge it is the first time that a sexual disparity in ground speeds has been identified in gliding birds. However, whether this is entirely due to a size-mediated difference in aerodynamic performance remains questionable; first, because sexual differences in V_g in all cases were greater than predicted (cf. Tables 2 and 3), and second, we did not take morphometrics from tracked birds, but rather assumed that they showed the same degree of sexual size dimorphism as the population as a whole. It is possible, therefore, that these differences arise partly or wholly from sexual variation in behavior.

Despite confirming the prediction that female albatrosses have lower ground speeds, and presumably therefore stall speeds, we found no compelling evidence to support the hypothesis that they are better adapted than males to flight in light winds (Shaffer et al. 2001). This hypothesis originally pertained to Wandering Albatrosses in the Indian Ocean, where colonies are located much closer to the belt of light winds associated with the subtropical high than is South Georgia (~1000 km vs. 2000 km). Black-browed, Gray-headed, and Wandering Albatrosses from South Georgia also exhibit some degree of sexual spatial segregation, with females tending to range at times through areas of lighter winds than males (Prince et al. 1998, Phillips et al. 2004, Xavier et al. 2004). Despite this, in all breeding stages we found no significant differences in the wind speeds experienced by males and females. Indeed, across species and sexes, wind speeds during foraging flights were very similar to mean wind speeds throughout the study area (7.6–8.2 m/s at $h_{ref} = 5$ m for the tracking periods). Hence, other explanations for spatial sexual segregation, such as competitive exclusion (Weimerskirch et al. 1993) and breeding role specialization (Weimerskirch et al. 2000a), should be reconsidered.

Diel and lunar phase.—To date, V_g of satellite-tracked albatrosses has been reported as being faster during daylight than darkness (Salamolard and Weimerskirch 1993, Walker et al. 1995, Phillips et al. 2005). Data from immersion loggers indicate that this is mainly because birds spend a greater proportion of their time in flight during daylight (70–80%) than darkness (20–40%) (Weimerskirch and Guionnet 2002, Phalan et al. 2007). Having corrected for this effect, we found that during direct uninterrupted bouts of flight, Wandering, Gray-headed, and Light-mantled Sooty Albatrosses all attained comparable V_g both day and night. Black-browed Albatrosses, however, flew slightly (0.9 m/s) faster during the day. It is not clear why this should be, because the activity patterns of this species are similar to those of the other species (Phalan et al. 2007). We were not able to test whether the V_g of Black-browed, Gray-

headed, and Light-mantled Sooty Albatrosses varied with lunar phase, because these species engaged in direct, sustained bouts of flight only on moonlit nights, reflecting the fact that they are more sedentary on moonless nights (Phalan et al. 2007). However, Wandering Albatrosses, which are also less active on moonless nights (Weimerskirch et al. 1997b), engaged in direct, sustained bouts of flight at comparable ground speeds on both moonlit and dark nights. Hence, low light levels do not inhibit flight in this species to the extent that V_g is reduced.

Flight direction with respect to wind and travel costs

There is still considerable debate about the theory of optimal ground speeds in central-place foraging birds (Hedenström and Ålerstam 1995, Hedenström et al. 2002, Houston 2006). However, one might hypothesize that albatrosses alter commuting speeds in response to the severity of the central-place constraint (Norberg 1981). Our results show that the V_g with respect to V_{wf} of albatrosses does not vary with breeding stage (models IIa–IIc). This is presumably because albatrosses rarely use flapping flight, which is the only obvious means by which they could increase their *airspeed* with respect to V_{wf} . As we have shown, however, *ground speed* is proportional to V_{wf} in all species. In Wandering Albatrosses, energetic expenditure (measured by the proxy heart rate) is proportional to the direction of flight with respect to wind θ_r (Weimerskirch et al. 2000b). Hence birds might reduce time and energy costs by choosing to fly only when the winds are relatively strong or from a favorable direction. Such behavior has been observed in both breeding and nonbreeding albatrosses (Murray et al. 2003, Catry et al. 2004a). However, we found no differences in wind speeds or directions experienced during different trip stages, so it is unlikely that such strategies predominate in the populations that we considered. This is perhaps unsurprising, given that South Georgia lies in the middle of the belt of strong, persistent westerly winds that prevail across the Southern Ocean between 35° and 65° S (Källberg et al. 2005) i.e., there may be insufficient variability in wind strength or direction to allow birds to be too selective about when they fly.

An alternative strategy would be to alter V_{wf} by altering flight direction with respect to wind, $\Delta\theta$. This could occur at the level of foraging trips or at smaller scales in response to changes in wind conditions encountered en route. For example, Wandering Albatrosses breeding in the Crozet Islands (46°25' S, 51°59' E) exploit large-scale semi-persistent wind patterns to make long, looping trips, avoiding headwind flight (Jouventin and Weimerskirch 1990, Weimerskirch et al. 2000b). Although the wind regime at South Georgia differs from that at Crozet, showing less variation in direction and strength with latitude (Källberg et al. 2005), birds from the populations that we studied also made long, looping flights during incubation and post-

brood (Phillips et al. 2004, 2005, Xavier et al. 2004; BAS, *unpublished data*). However, this strategy is apparently either not always effective or preferable because birds frequently encountered headwinds during outward trips and tailwinds on their return. This trend was most marked in the brood-guard stage Wandering Albatrosses and least so in incubating Gray-headed Albatrosses. The difference probably reflects the severity of the central-place constraint. The dominant response of albatrosses to the increase in this constraint following hatching is to reduce foraging range, with birds making shorter, direct trips to discrete areas (Shaffer et al. 2003). This may leave them with less choice in their flight direction with respect to wind than during the incubation or post-brood stages (Salamolard and Weimerskirch 1993). At South Georgia, where brood-guard stage Wandering Albatrosses forage to the west colony (Prince et al. 1998), birds therefore encounter headwinds during the outward stages of trips. In the middle stages of foraging trips, when they were less constrained, all species tended to fly most often with side winds. Hence, flight direction with respect to wind is a function of both preference and the relative locations of the colony and foraging areas (Spear and Ainley 1997a).

Clearly this has implications for both the time and energetic costs of foraging trips (Salamolard and Weimerskirch 1993). Within the range of wind speeds typically encountered by birds in our study ($\bar{V}_{w5} \approx 8 \pm 5$ m/s, mean \pm SD), variability in ground speed due to relative flight direction was greater than that due to changes in wind speed. For example, a Black-browed Albatross in downwind flight would only experience a $1.4\times$ (5.3 m/s) increase in ground speed if the wind speed increased from 3 to 13 m/s, decreasing journey time by 6.3 h over 1000 km. In contrast, the same bird flying in winds of \bar{V}_{w5} would experience a $2.1\times$ (8.5 m/s) increase in ground speed by turning from headwind to tailwind flight. This corresponds to a decrease in journey time of 21.6 h over 1000 km. However, we did not observe such a large difference in outward and return V_g in those species that foraged upwind of South Georgia (Wandering, Black-browed, and Light-mantled Sooty Albatrosses; Prince et al. 1998, Phillips et al. 2004, 2005). Ground speeds of these species were, on average, 1.0, 1.4, and 1.2 m/s faster, respectively, during return trips. This indicates that birds are able to use the behavioral strategies just outlined to buffer against the effects of wind.

Given that albatross $V_g \sim V_{wf}$, it is interesting to speculate on the effect of this on habitat accessibility during breeding. Clearly, wind allows birds in some areas, such as the Indian Ocean, to complete long foraging trips, accessing distant resources (Jouventin and Weimerskirch 1990, Weimerskirch et al. 2000b). In contrast, birds foraging from South Georgia are subject to a more uniform wind field. Pennycuik (1989) predicted that the energetic cost of foraging trips made by flapping birds in such an environment would be lower

if they foraged upwind rather than downwind of the colony. Similarly, if the energetic cost of flight increases as an albatross gains body mass during a chick-provisioning trip (for example by reducing the efficiency of dynamic soaring), it may be more efficient to make such trips upwind of the colony. This type of mechanism could explain in part why albatrosses from South Georgia rarely forage to the east (downwind) of the islands (Prince et al. 1998, Phillips et al. 2004, 2005).

Despite the complexity of their flight patterns, we have demonstrated that the ground speeds of albatrosses can be predicted by considering morphology and relative wind. We suggest that the birds may reduce transport costs by (1) flying only when winds are of a favorable strength or direction; (2) routing their foraging trips to exploit large-scale wind patterns; or (3) altering flight direction with respect to wind in response to changing wind conditions during trips. Downwind or crosswind flight is preferred, but in some circumstances the additional costs of traveling upwind may be outweighed by rapidly gaining access to resources. Hence, during breeding, when birds are constrained to return regularly to the colony, habitat accessibility should be regarded as a function of both distance from the colony (Matthiopoulos 2003) and wind field. We hope that our findings will stimulate further research into the effects of wind on seabirds such as albatrosses in different wind regimes, especially given the fact that large-scale wind patterns are projected to alter across the Southern Ocean over the next century as a result of human-induced climate change (Shindell and Schmidt 2004, Bracegirdle et al. 2008).

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APPENDIX A

Instrument deployment details for albatrosses tracked from Bird Island, South Georgia during the 2001–2004 breeding seasons (*Ecological Archives* M079-024-A1).

APPENDIX B

Division of foraging trips into outward, middle, and inward stages (*Ecological Archives* M079-024-A2).

APPENDIX C

Estimation of minimum distance between ARGOS locations (*Ecological Archives* M079-024-A3).