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Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements

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SUMMARY

A tracking radar and an optical range-finder, placed on a ship, were used to register the flight of eleven species of seabirds, in waters off the Antarctic Peninsula and in the Atlantic Ocean.

Albatrosses under calm conditions used swell soaring, turning and twisting extensively within a width of 300–500 m laterally from the overall direction of movement. Their resulting travel speed was on average 10 m s^{-1}. In windy conditions the albatrosses as well as giant petrels travelled faster, with resulting speeds up to 22.5 m s^{-1}, by a combination of wave soaring and dynamic soaring.

Shearwaters and the antarctic fulmar proceeded by flap-gliding, along tracks that were only slightly zigzag within 50–60 m from the resulting course of movement. The little shearwater flew faster, with an airspeed about 14 m s^{-1}, than larger-sized shearwaters and fulmars, using continuous flapping flight to a higher degree than its larger relatives.

South polar skuas and Wilson's storm-petrels were tracked on foraging flights, and flocks of imperial shags on commuting flights between feeding and breeding–roosting areas. The south polar skua was able to accelerate to airspeeds exceeding 20 m s^{-1} in pursuit flights after shags. Wilson's storm-petrels showed significantly slower airspeeds in foraging flights as compared to non-foraging flights.

Average airspeeds of most species fell between the minimum power and maximum range speeds estimated from aerodynamical theory. Species using gliding or flap-gliding flight showed a mean airspeed close to the gliding speed for best glide ratio. Optimal speeds in foraging flights, as expected for the south polar skuas and Wilson's storm-petrels, are unlikely to coincide with the minimum power and maximum range speeds.

Albatrosses reached the fastest resulting travel speeds when moving at angles 120°–150° from the wind (partly following winds), with strong wind forces. They predominantly travelled with the wind from their left side which, in the southern hemisphere, would lead them away from low pressure centres and towards high pressure areas.

1. INTRODUCTION

The aerodynamical principles of seabird flight have since long attracted theoretical attention. Different ways of extracting energy from the wind by static (soaring in updrafts along waves and swells) and dynamic soaring are used in different combinations depending on species and on wind and wave conditions (Idrac 1924; Cone 1964; Wilson 1975; Pennycuick 1982).

How do the seabirds using these flight techniques perform with respect to travelling paths and speeds under different winds? How do their flight speeds compare with the characteristic flapping and gliding speeds predicted from the aerodynamical theory of bird flight (Pennycuick 1989)? Increased knowledge about these questions will help to judge better the seabirds' capacities of travelling over the open sea and to clarify how they move in relation to weather and wind systems.

Fine-scale measurements of the flight of both southern and northern seabirds have been presented and analysed by Pennycuick (1982, 1987). These data were recorded by ornithodolite (an optical range-finder equipped for simultaneous recording and storage of range, azimuth and elevation to the bird target) over flight distances of a few hundred metres with high time resolution (a few seconds between successive position readings).

On a much wider scale, successful satellite tracking of the most large-sized seabirds, southern giant petrels *Macronectes giganteus* and wandering albatrosses *Diomedea exulans*, has recently been accomplished (Strikwerda *et al.* 1986; Jouventin & Weimerskirch 1990; Prince *et al.* 1992). The wandering albatrosses were tracked during oceanic flight journeys lasting 3–33 days when the birds covered several thousands of kilometres, up to 15000 km, in a single foraging trip before returning to the nest. The time interval between successive satellite locations of a bird with transmitter was at least 90 min.

In this study we have used tracking radar to obtain

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detailed observations of seabird flight paths and speeds over typical distances of a few kilometres. We made supplementary measurements by an optical range-finder useful for tracking the birds over similarly long distances under windy conditions, when the radar could not be effectively used because of sea clutter interference. The radar and optical instrument were placed on the deck of the Swedish expedition ship M/V *Stena Arctica*, and observations were carried out in waters at the Antarctic Peninsula, and in the Atlantic Ocean on the ship's return journey from Antarctica to Sweden.

In this paper we will present and analyse our tracking results to throw light on the questions mentioned above. Observations at different levels of spatial and temporal resolution, by optical instruments, radar and satellite telemetry, are to a high degree complementary to each other in the process of gaining increased insight about the possibilities and limitations of seabird flight and migration performance.

2. METHODS, SPECIES AND STUDY AREAS

(*a*) *Equipment and calculations*

The tracking radar (X-band, peak power 40 kW, pulse duration 0.3 μs, pulse repeat frequency 1800 Hz, pencil beam width 2.2°) was placed on the top deck (above the bridge) of the ship M/V *Stena Arctica* (Swedish expedition SWEDARP 1988/89), with its antenna at 26 m above sea level (ASL). Range, elevation and bearing to the target were automatically read from the radar and stored by computer every 3, 5 or 10 s. The radar is equipped with 9 × and 18 × binoculars which permit the two operators to identify the targets and report the birds' flight behaviour to a tape recorder simultaneously with the computer registrations.

During tracking the radar was operated in automatic tracking mode with respect to the distance to the target, while azimuth and elevation angles were normally controlled manually through the telescopic sight. This method was more precise than automatic angular tracking, because of the rapidly shifting courses and flight manoeuvres by many of the seabirds. Individual birds were tracked at ranges 0.3–3 km from the radar (only the shags were tracked while flying in flocks). Maximum error during automatic tracking of a target in high speed motion at 1 km distance is ±0.7° in elevation and azimuth and ±12 m in range.

The radar was effective in recording the birds' flight over a smooth sea surface, under near calm conditions (wind speed less than 4 m s^{-1}). However, in more windy situations, and where there were many ice-floes, sea- and ice-clutter on the radar indicator prevented successful bird tracking near the sea surface.

Under these conditions we used our optical range finder (WILD, 80 cm, 11.25 ×) supplemented with azimuth and elevation scales, to determine positions of seabirds normally at 0.3–3 km range. Time intervals between readings were irregular because accurate range measurements were temporarily impossible due to the rolling of the ship and to wind gusts, and also when the birds disappeared in wave-troughs. On average, the time interval between successive readings was 25 s. During optical tracking, one operator followed the target bird through the instrument, reporting range measurements to a second operator who then made simultaneous readings of time and azimuth angle to the nearest second and degree, respectively. Elevation angle was not recorded, because it was often greatly affected by the rolling movements of the ship. Consequently, positions from the optical tracking data were determined in two dimensions only. However, this does not introduce any important error since all birds were tracked while flying within a few tens of meters above the sea surface. Ground-based calibration measurements to fixed objects at known distances, indicated that our optical range measurements were accurate to within ±10 m for a target at 500 m distance, ±20 m at 1 km and ±100 m at 2 km distance.

Trackings refer to birds flying over the sea and moving clear of the ship. We did not track birds following the ship, flying in its wake or at distances within 300 m from the ship (this was the minimum recording range for the radar as well as the optical instrument).

Weather was recorded and stored on computer every 30 min around the clock from an automatic weather station on the upper deck with the wind vane and anemometer mounted on the highest mast, 38 m ASL. Current wind and weather data, updated every 10 min, were also available directly from the computer screen. For each tracking, we recorded the current data for the wind and for the ship's direction and speed. Trackings were carried out both when the ship was stationary and when moving at constant courses and speeds up to 14 knots.

Because directions and speeds obtained from the anemometer were measured relative to the ship, the true wind directions and speeds must be calculated by taking the ship's orientation and movement into account, through vector addition. Likewise, the ship's direction and speed was taken into account to calculate the true flight paths and velocities relative to geographic north and to the 'ground' (i.e. relative to a stationary object on the earth's surface) from the tracking data.

Average groundspeed was calculated for each tracking by dividing the cumulative distance along the flight path by the total tracking time. Many sea birds show typical irregularities in their flight paths although they are clearly making headway in a consistent overall direction. As a measure of straightness for the flight paths we calculated the ratio of straight-line distance between the initial and final tracking position to the cumulative distance between all successive positions along the flight path. This was not applied to curved tracks where the birds clearly changed their overall direction of resulting movement.

To estimate wind speed at the altitude where the birds were flying, the wind speed measured (at 38 m ASL) was multiplied by a wind factor according to the classical wind gradient equation (cf. Pennycuick

1982). Under near-calm conditions (radar trackings), a wind factor of 0.55 was used for flights extremely low, about 0.1 m, over the sea surface (most of the trackings of Wilson's storm-petrel, cf. table 1 and 2), 0.7 was used for low level flight about 0.5–1 m above the sea (most species), while a factor of 1.0 was adopted for flights between 10 and 50 m ASL (south polar skua). Under conditions of a medium-rough sea (optical trackings), a wind factor of 0.7 was used for birds flying mainly about 1–2 m above the waves (shearwaters and fulmar), 0.85 for birds flying at varying altitudes (descents alternating with pull-ups) around a mean about 5–10 m ASL (albatrosses, giant petrel), and 1.0 for birds flying higher than this (south polar skua). Wind direction was assumed to be constant across altitudes.

Airspeeds of birds were calculated by vector subtraction of the wind velocity from the birds' flight vector in relation to the ground (track direction/groundspeed). Airspeeds were determined for each interval between measured positions, and the average airspeed for each tracking was calculated by dividing the cumulative flight distance relative to the air by the total tracking time. Wind speeds given in the text refer to the wind at 38 m ASL.

(*b*) *Species and study areas*

Species included in this study are presented in table 1, along with estimated typical mean body masses, wingspans and aspect ratios (= wing span^2/wing area, with wing area measurement as defined by Pennycuick (1989)). The latter data were taken from Pennycuick (1982, 1987), with complementary information from Warham (1977), Cramp & Simmons (1977), Harrison (1985) and Furness (1987). For great shearwater and south polar skua there are no available measurements of wing area, and the aspect ratio has been provisionally estimated to conform with that in similar-sized shearwaters and fulmars (great shearwater) and in the great skua (south polar skua).

Only trackings with at least four position fixes are included in the analysis, and at least three trackings are available for each species.

The data were obtained mainly in Antarctic waters, along the west coast of the Antarctic Peninsula and at the South Shetland Islands between 61–68°S, during the period 23 February–17 March 1989 (southern giant petrel, black-browed and grey-headed albatross, antarctic fulmar, Wilson's storm-petrel, south polar skua and imperial shag). Furthermore, during the ship's return voyage to Europe, additional data were obtained in the Atlantic Ocean off the coast of South America between 34–50°S on 20–25 March (black-browed and yellow-nosed albatross, great and little shearwater), and off Madeira at 32°N on 11 April 1989 (Cory's shearwater).

The albatrosses, great and little shearwaters and most antarctic fulmars were tracked far offshore, 30–200 km from the nearest land. In contrast, most giant petrels, Wilson's storm-petrels, south polar skuas and imperial shags were registered only 2–10 km off the nearest shorelines in the Palmer Archipelago (64°10′S, 61°50′W), Marguerite Bay (67°50′S, 67°30′W; see also Gudmundsson *et al.* (1992)) and the South Shetland Islands (61–63°S, 55–61°W). Cory's shearwaters were tracked while flying north in an area extending 100 km south of Madeira.

Temperatures in the Antarctic region ranged between $-1°$ and $+4°$C, off South America between 10 and 22°C and at Madeira it was 18°C. Flight is affected by the air density, which varies with temperature and barometric pressure. The air density at sea level varied between 1.23 and 1.28 kg m^{-3} (mean 1.25 kg m^{-3}) for the trackings in the Antarctic region, between 1.19 and 1.23 kg m^{-3} (mean 1.21 kg m^{-3}) off South America, and it was 1.24 kg m^{-3} at Madeira. For calculations according to Pennycuick's (1989) programmes for bird flight we have used an overall mean air density of 1.23 kg m^{-3}.

3. RESULTS

(*a*) *Flight speeds*

Altogether 192 trackings of the eleven study species were recorded, 89 of which were radar trackings and 103 optical trackings (table 2). The radar trackings

Table 1. *Study species with estimated average body measurements*

species	mass/kg	wingspan/m	aspect ratio
Procellariiformes			
1. southern giant petrel (*Macronectes giganteus*)	5.19	1.99	12.0
2. black-browed albatross (*Diomedea melanophris*)	3.79	2.16	13.1
3. grey-headed albatross (*Diomedea chrysostoma*)	3.79	2.18	13.5
4. yellow-nosed albatross (*Diomedea chlororhynchos*)	2.07	1.91	13.2
5. Cory's shearwater (*Calonectris diomedea*)	0.946	1.21	11.9
6. antarctic fulmar (*Fulmarus glacialoides*)	0.887	1.17	10.6
7. great shearwater (*Puffinus gravis*)	0.834	1.05	(*ca.* 11)
8. little shearwater (*Puffinus assimilis*)	0.238	0.60	8.4
9. Wilson's storm-petral (*Oceanites oceanicus*)	0.038	0.39	8.0
other seabirds			
10. south polar skua (*Catharacta maccormicki*)	1.32	1.27	(*ca.* 8.8)
11. imperial shag (*Phalacrocorax atriceps*)	2.23	1.13	7.0

Table 2. *Numbers of radar and optical trackings, and the associated numbers of position measurements, total times and distances*

	radar				optical range-finder			
species	no. of trackings	no. of fixes	total tracking time/s	total tracking distance/m	no. of trackings	no. of fixes	total tracking time/s	total tracking distance/m
southern giant petrel	3	55	375	5010	23	171	3959	44 125
black-browed albatross	5	79	670	8519	19	148	3371	42 834
grey-headed albatross	11	355	2097	26 644	—	—	—	—
yellow-nosed albatross	6	199	965	11 023	7	40	725	9684
Cory's shearwater	—	—	—	—	16	179	3512	29 457
antarctic fulmar	3	44	290	2701	11	69	1798	19 923
great shearwater	13	209	980	10 715	—	—	—	—
little shearwater	3	61	290	4225	—	—	—	—
Wilson's storm-petrel	14	161	1375	8985	—	—	—	—
south polar skua	22	467	3630	47 224	27	223	5369	59 748
imperial shag	9	126	1170	17 664	—	—	—	—

sum up to a total tracking time of 3.3 h, during which time the seabirds were flying over a total distance of 143 km (relative to the ground). The corresponding total time and distance for the optical trackings are 5.2 h and 206 km, respectively. Because of the finer time resolution for the radar data (position measurements with regular intervals of either 5 s or 10 s and in one case 3 s) the number of fixes are much larger (total number of radar fixes = 1756) than for the optical data (total number of optical fixes = 830).

Flight speeds of the seabirds as recorded by radar under near-calm conditions (wind speed at 38 m ASL $\leqslant 4$ m s^{-1}) are presented in table 3. Mean wind speeds (at 38 m ASL) associated with the radar trackings were between 1.1 and 3.0 m s^{-1} for the different species. Because of the low wind forces, the speed increments caused by wind (groundspeed minus airspeed; cf. Pennycuick 1987) are small. Sample sizes for the data in table 3 are the number of trackings given for each species in table 2. The standard deviation has been omitted for the two species with a sample size of only three trackings.

The data in table 3 refer to birds flying over a smooth or only slightly rippled open sea surface, although often with significant swells. Wilson's storm-petrel showed the slowest mean airspeed, 7.4 m s^{-1}, whereas the imperial shags were the fastest flyers with a mean airspeed of 16.4 m s^{-1}. The three species of albatrosses flew with similar airspeeds, 12–13 m s^{-1}, using almost pure gliding flight over the swells, while the giant petrels reached slightly faster airspeeds by flap-gliding (cf. Pennycuick 1982). The little shearwater, using steady flapping flight, flew much more rapidly than the antarctic fulmar and great shearwater which resorted more to flap-gliding.

The largest variation in airspeed was found in Wilson's storm-petrel (Coefficient of variation = 26%) and south polar skua (CV = 13%), while the scatter was smallest for the imperial shag. The flight paths of albatrosses and giant petrels showed the highest degree of zigzag irregularities (straightness 0.78–0.84). The fulmar, shearwaters and storm-petrel were intermediary in this respect (straightness 0.90–0.94), while the south polar skua and particularly the imperial shag flew along almost rectilinear paths.

Flight speeds of the seabirds under mainly windy conditions, as determined from the optical trackings, are presented in table 4. Sample sizes are found in table 2. Wind speeds (at 38 m ASL) were mainly in the range 5–20 m s^{-1}, although a few optical trackings were made at wind speeds below this range. The average wind speeds fell in the range 10–13 m s^{-1} for the optical trackings of the two albatross species and the giant petrel, and in the range 6–8 m s^{-1} for the other three species. The giant petrels, Cory's shearwaters and, to a lesser extent, the south polar skuas, were tracked most often while flying into headwinds, as shown by the substantial negative mean speed increment caused by wind.

The groundspeeds of the seabirds were of course greatly affected by the wind, varying from 4.3 to 25.0 m s^{-1} for the different trackings depending on whether the birds were making headway into opposing winds or if they were travelling with wind assistance. Flight paths of albatrosses and giant petrels were more irregular than those of the shearwaters, fulmars and skuas. It should be noted that the straightness indices calculated for the optical trackings are not directly comparable with those based on the radar data. The finer time resolution in the latter data makes it possible to reveal fine-scale irregularities in the flight paths that will be missed in the optical tracking data. For this reason, the optical trackings are expected to show larger straightness indices than the radar data, unless the birds introduce relatively large-scale irregularities in their flight paths under windy conditions.

Birds travelling by flapping flight are expected to increase their airspeed when flying into headwinds or reduce it when flying with tailwinds in order to minimize the energy costs per unit of distance covered (Pennycuick 1978). This was investigated by calculating linear regressions of the airspeed in relation to the speed increment caused by wind, i.e. groundspeed minus airspeed, as summarized in table 5. In this analysis, we have used airspeed estimates from both the radar and optical tracking data. Furthermore, we

Table 3. *Flight speeds of seabirds tracked by radar under near-calm conditions*

	groundspeed/(m s^{-1})			airspeed/(m s^{-1})			speed increment from wind/(m s^{-1})		straightness	
species	mean	s.d.	range	mean	s.d.	range	mean	s.d.	mean	s.d.
southern giant petrel	13.3	—	12.4–14.4	14.5	—	13.5–15.2	−1.2	—	0.84	—
black-browed albatross	12.9	1.7	11.2–15.6	12.7	1.2	11.2–14.3	0.1	0.7	0.82	0.09
grey-headed albatross	13.2	1.5	11.0–15.5	13.0	1.2	11.3–15.1	0.2	1.1	0.84	0.11
yellow-nosed albatross	11.1	1.0	9.9–12.4	12.0	1.0	11.2–13.8	−0.9	0.7	0.78	0.09
antarctic fulmar	9.4	—	8.0–10.9	10.6	—	9.2–11.5	−1.2	—	0.94	—
great shearwater	10.8	1.4	8.9–13.1	10.8	1.3	9.4–13.2	0.0	0.5	0.94	0.05
little shearwater	14.4	—	14.0–14.9	14.4	—	14.2–14.5	0.0	—	0.94	—
Wilson's storm-petrel	7.1	1.9	4.4–10.8	7.4	1.9	4.7–10.0	−0.3	1.0	0.90	0.08
south polar skua	13.0	1.9	8.9–16.3	13.1	1.7	11.0–16.8	0.0	2.0	0.97	0.03
imperial shag	15.3	0.8	13.9–16.4	16.4	0.9	15.2–17.6	−1.1	0.6	0.99	0.01

Table 4. *Flight speeds of seabirds under variable wind conditions, as measured by optical tracking*

	groundspeed/(m s^{-1})			airspeed/(m s^{-1})			speed increment from wind/(m s^{-1})		straightness	
species	mean	s.d.	range	mean	s.d.	range	mean	s.d.	mean	s.d.
southern giant petrel	11.8	3.2	4.9–17.4	16.3	3.3	8.6–22.0	−4.5	5.0	0.91	0.09
black-browed albatross	12.9	5.0	7.7–25.0	13.4	2.9	9.0–19.6	−0.5	3.9	0.92	0.07
yellow-nosed albatross	12.5	5.9	4.3–21.2	10.8	1.8	9.0–14.0	1.7	5.2	0.96	0.04
Cory's shearwater	8.6	1.3	6.0–11.0	13.2	0.7	11.9–14.3	−4.6	1.3	0.96	0.03
antarctic fulmar	10.5	3.0	6.2–15.6	9.8	2.4	5.8–12.8	0.6	1.4	0.96	0.04
south polar skua	11.6	3.8	6.6–19.6	13.8	2.9	9.7–21.4	−2.3	4.6	0.96	0.04

Table 5. *Effect of wind on the birds' airspeed*

(Calculated linear regression data for the airspeed (m s^{-1}) in relation to speed increment caused by wind (groundspeed minus airspeed; m s^{-1}) in four different species or categories of seabirds.)

species	intercept (m s^{-1})	slope	s.e. of slope	corr. coeff.	n	p
southern giant petrel	14.0	−0.51	0.08	−0.78	26	<0.001
albatrosses[a]	12.5	0.00	0.10	0.00	48	NS
shearwaters/fulmar[b]	10.6	−0.48	0.10	−0.62	43	<0.001
south polar skua	13.0	−0.37	0.08	−0.57	49	<0.001

[a] Data for three species combined: black-browed, grey-headed and yellow-nosed albatross.

[b] Data for three similar-sized species combined: Cory's and great shearwater, and antarctic fulmar.

have combined data for the three albatross species into one category, and for the three similar-sized species of shearwater and fulmar into another category, to obtain sufficient data over a wide range of wind conditions.

Wilson's storm-petrel and imperial shag were tracked only under a narrow range of near-calm conditions, and although both species showed a negative regression coefficient for the airspeed in relation to the wind increment (−0.52 and −0.72, respectively), the correlations were not statistically significant ($p > 0.05$) and data for these species have been excluded from table 5.

The southern giant petrel, shearwaters/fulmar and south polar skua showed a highly significant effect of wind on the airspeed, but there was no such relationship in the albatrosses (table 5). The variation in airspeed was analysed within a range of speed increment due to wind from −11.1 to +5.1 m s^{-1} for the southern giant petrel, from −6.3 to +7.2 m s^{-1} for the albatrosses, from −6.6 to +4.1 m s^{-1} for the shearwaters/fulmar and from −13.7 to +6.5 m s^{-1} for the south polar skua.

The relationship between airspeed and wind for the shearwaters/fulmar must be considered as tentative, as it arises mainly as a consequence of the difference in airspeed between the Cory's shearwaters flying into headwinds and the great shearwaters/antarctic fulmars tracked under relatively calm conditions (cf. tables 3 and 4). However, it seems plausible that these species because of their similarity in size, wing morphology and behaviour, fly at closely similar airspeeds and respond to wind in the same way.

The absence of any wind effect on the airspeed of the albatrosses is supported by the fact that neither of the three species, when considered alone, showed any significant correlation between airspeed and speed increment caused by wind. In contrast to the other species, the albatrosses were observed to proceed by almost pure gliding flight under all wind conditions.

(*b*) *Flight behaviour and tracks*

(i) *Albatrosses*

Under near-calm conditions the albatrosses glided at the lowest possible level over smooth but sizeable swells. Only occasional wingbeats were seen. Some of the yellow-nosed albatrosses flapped their wings a bit more often, partly proceeding by regular flap-gliding. The flight tracks were very irregular and winding as the albatrosses twisted and turned within a width of approximately 300–500 m laterally from their overall direction of movement (figure 1).

Under windy conditions the albatrosses used pure gliding flight, alternating in a characteristic way between climbs up to 10–30 m ASL and descents in the wave-troughs. The optical trackings do not reveal the fine-scale movements during this cycle as positions were mainly determined when the birds were close to their altitudinal culmination points.

Under crosswinds the resulting tracks, as determined by optical measurements, were rather straight (figure 2*e*, *f*). In contrast, under opposed or following winds the albatrosses tacked several hundred meters to and fro across their resulting course of movement, proceeding by a large-scale cruising pattern superimposed upon the fine-scale climb–descent cycles mentioned above (figure 2*a*,*g*).

In the albatross tracking showed in figure 2*g*, an additional cycle of sideways cruising movement almost certainly occurred in the long time interval between the second last (at 168 s) and last position (at 274 s; in this time interval we failed to attain accurate position measurements). The extensive cruising manoeuvres had the effect of slowing down the resulting 'cross-country' groundspeed (from initial to final position) for this track to 13.0 m s^{-1} (the tailwind force was 19.3 m s^{-1}).

(ii) *Southern giant petrel*

This species proceeded by flap-gliding (wingbeat periods alternating with gliding) to a higher degree than the albatrosses. This was the typical flight mode under calm conditions; in windy weather they periodically flapped their wings, although they also glided extensively. Generally they did not soar so high over the waves as did the albatrosses. In contrast to the albatrosses which were tracked over the open ocean most giant petrels were registered in coastal waters not far from their breeding colonies. Many of them travelled in brisk headwinds, showing zigzag cruising tracks that were similar to those of albatrosses in this situation (figure 2*b*–*d*).

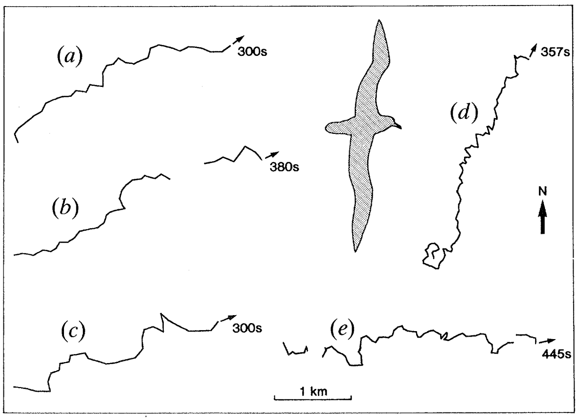

Figure 1. Flight tracks of albatrosses over the open sea under near-calm conditions, as recorded by radar. (*a*) Black-browed albatross, (*b*)–(*d*) grey-headed albatross and (*e*) yellow-nosed albatross. The time interval between successive position measurements is 10 s in (*a*)–(*c*), 3 s in (*d*) and 5 s in (*e*). The total tracking time is indicated. Temporary breaks in radar registration of the target show up as gaps in the tracks. The track in (*d*) starts just as the albatross takes off from the sea surface.

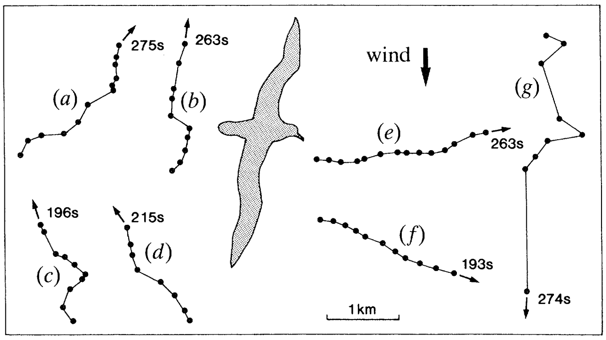

Figure 2. Flight tracks of albatrosses and southern giant petrels over the sea under windy conditions, as recorded by optical measurements. Time intervals between position measurements (dots) are irregular. (*a*) Black-browed albatross (wind speed 8.9 m s^{-1}), (*b*)–(*d*) southern giant petrel (wind speed 11.4, 11.4 and 11.9 m s^{-1}, respectively), (*e*)–(*g*) black-browed albatross (wind speed 11.7, 11.7 and 19.3 m s^{-1}, respectively). Flights in headwinds are examplified in (*a*)–(*d*), in crosswinds in (*e*)–(*f*) and in following winds in (*g*).

(iii) *Shearwaters and antarctic fulmar*

In calm weather the great shearwaters and antarctic fulmars travelled by flap-gliding, characterized by relatively long wingbeat periods and short gliding intervals. Banking a bit to the right and left as they flew low over the sea surface, their resulting tracks were slightly zigzag within a flight corridor width of approximately 50–60 m transverse to their direction of movement (figure 3). In contrast to their larger relatives, the little shearwaters proceeded by rapid and continuous flapping flight, rather like auks.

Cory's shearwaters showed forceful flapping flight with only very short gliding intervals, when travelling into headwinds within a few meters above the waves. They frequently banked to the right and left, and the resulting tracks were slightly irregular (figure 4). In other winds and when following the ship the Cory's shearwaters were seen to glide a lot more. Relatively more gliding, interspersed with regular flapping periods, was also evident in antarctic fulmars making effective progress in following crosswinds (figure 4*e*, *f*).

(iv) *Wilson's storm-petrel*

This small species fluttered with quick wingbeats at the lowest possible level over the sea surface, making sudden banking and gliding manoeuvres. Some of the storm-petrels were seen to pick food repeatedly from

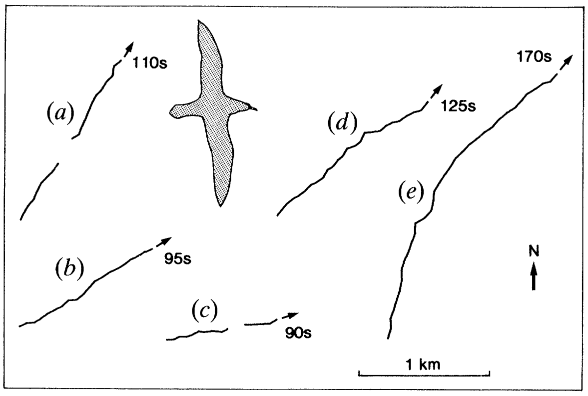

Figure 3. Flight tracks of shearwaters over the sea under near-calm conditions, as recorded by radar. (*a*)–(*d*) Great shearwater and (*e*) little shearwater. The time interval between successive position measurements is 5 s for all trackings.

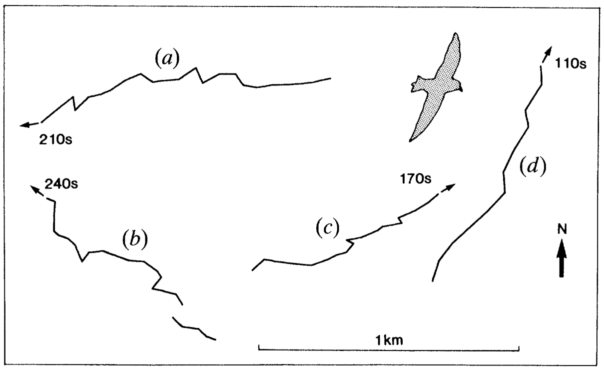

Figure 5. Flight tracks of Wilson's storm-petrel over the sea under near-calm conditions, as recorded by radar. The time interval between successive position measurements is 10 s for all trackings. Foraging flights, where the bird picked food from the water surface a number of times, are shown in (*a*)–(*c*), while no foraging was observed in (*d*).

the water surface, briefly hovering or even landing a second or two while picking, only to fly off immediately again (figure 5*a*–*c*). In other cases, the birds proceeded virtually without food picking, sometimes flying some decimetres above the sea surface (figure 5*d*).

Distinguishing between such foraging and non-foraging flights (probably corresponding to flights within and between food patches, respectively), as in figure 6, shows that airspeeds are significantly ($p < 0.001$) slower during the foraging flights (mean airspeed $= 5.5$ m s^{-1}, s.d. $= 0.7$ m s^{-1}, $n = 6$) as compared to the transportation flights (mean airspeed $=$ 8.8 m s^{-1}, s.d. $= 1.1$ m s^{-1}, $n = 8$). Part of this difference is due to reduced flight speeds during the food picking events. The airspeed in 10 s intervals with observed food pickings ranged between 2.5–5.1 m s^{-1} ($n = 13$ exactly timed events of food picking). However, in most 10 s intervals of the foraging flights there were no food pickings and still the airspeed was in a range (mostly 4–8 m s^{-1}) clearly below airspeeds that were regularly attained during non-foraging flights (often 8–11 m s^{-1}). There was a significant correlation between mean airspeed and straightness of the tracks ($r = 0.73$, $n = 11$, $p = 0.01$), and the straightness was on average significantly ($p < 0.01$) lower for the foraging tracks (mean $= 0.84$) than for the non-foraging tracks (mean $= 0.95$).

(v) *South polar skua*

Most skuas were tracked while patrolling for food, surveying the sea beneath them as they flew by steady flapping flight at altitudes between 10 and 40 m (mean altitude for the radar trackings in calm weather was 23 m ASL). Flight paths were often curved as the skuas changed courses from time to time, searching around icebergs or floes.

There was a peak of airspeeds in the range 11–14 m s^{-1}, but also quite a number of cases where the skuas flew at 14–18 m s^{-1}. Some of these faster airspeeds were of birds flying into headwinds (table 5),

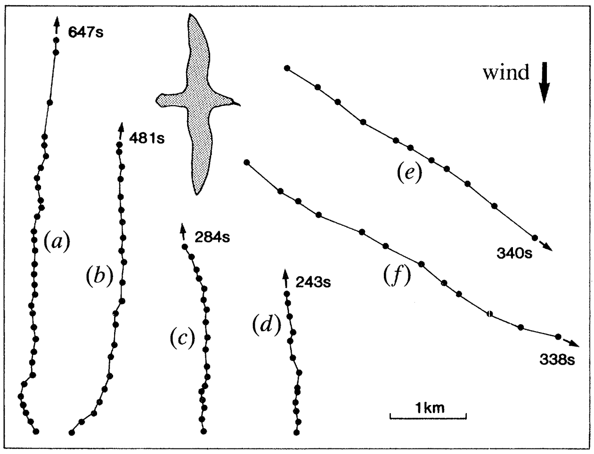

Figure 4. Flight tracks of Cory's shearwater and antarctic fulmar over the sea under windy conditions, as recorded by optical measurements. (*a*)–(*d*) Cory's shearwater (wind speed 9.0, 8.1, 5.2 and 7.4 m s^{-1}, respectively), (*e*)–(*f*) antarctic fulmar (wind speed 12.6 and 12.3 m s^{-1}, respectively). Flights into headwinds are shown in (*a*)–(*d*) and with following crosswinds in (*e*)–(*f*).

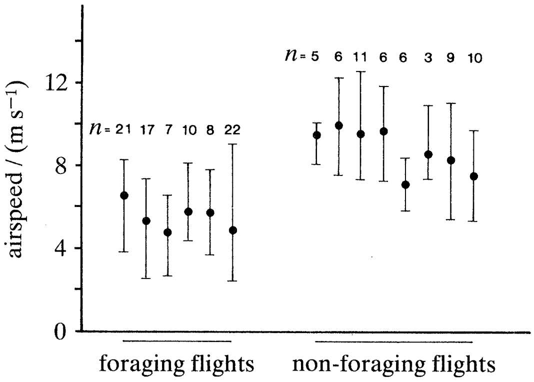

Figure 6. Airspeeds (range and mean) during 5 or 10 s time intervals, calculated on the basis of radar trackings of foraging (several pickings of food from water surface observed) and non-foraging flights of Wilson's storm-petrel. Number of time intervals with speed data (n) are indicated for each tracking.

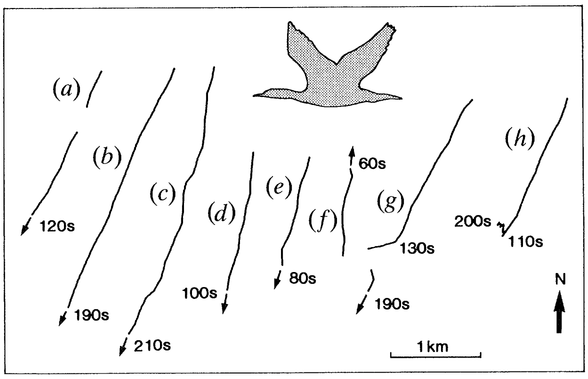

Figure 7. Flight tracks of imperial shags and south polar skua over the sea under near-calm conditions, as recorded by radar. (*a*)–(*g*) Imperial shag and (*h*) south polar skua. The time interval between successive position measurements is 10 s for all trackings. All tracks are from Marguerite Bay and for the shags they refer to local commuting flights between feeding and breeding–roosting areas. The track of a pair of shags attacked by a south polar skua is shown in (*g*), whereas (*h*) shows a kleptoparasitic pursuit flight of a south polar skua catching up with an imperial shag (cf. figure 8).

while other cases, not in headwind situations, may refer to transportation flights between feeding waters and nesting sites.

The skuas were also repeatedly seen to accelerate in successful pursuit flights after flying shags from several hundred metres behind. One radar tracking of such a skua pursuit flight was recorded (figure 7*h*, 8). In this case the skua accelerated from its patrolling flight speed to almost 22 $\mathrm{m\,s^{-1}}$ over a period of 70 s (mean acceleration 0.14 $\mathrm{m\,s^{-2}}$ with a peak of 0.49 $\mathrm{m\,s^{-2}}$ during the initial 10 s). The skua flew with very forceful and vigourous wing-beats during this phase of acceleration. A considerable fraction of the increase in kinetic energy (about 220 J) was probably regained from the loss of potential energy as the skua descended from about 15 m ASL to low over the water surface during the initial 40 s of this pursuit flight. After the acceleration phase the skua manoeuvred and climbed briefly in order to dive violently towards the shag (after 100 s). The latter responded by landing and diving into the water with the skua flying overhead and diving at it as soon as it surfaced (two additional skuas joined in these diving attacks). After 200 s the skua finally settled on the water, probably collecting food regurgitated by the shag.

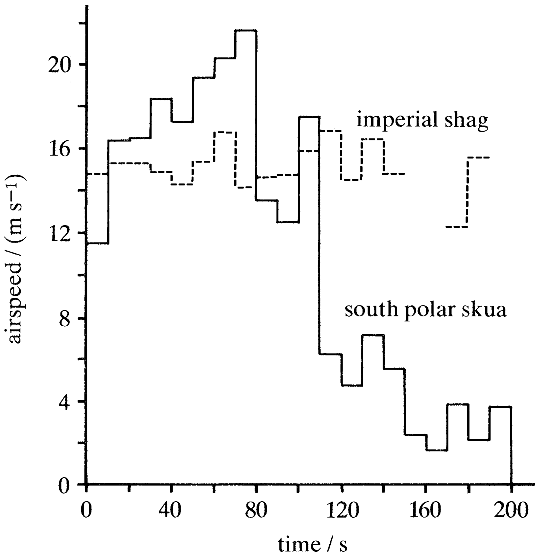

Figure 8. Airspeed during successive 10 s time intervals for a pair of imperial shags pursued and attacked by a south polar skua (track (*g*) in figure 7), and for a south polar skua in kleptoparasitic pursuit flight of an imperial shag (track (*h*) in figure 7).

(vi) *Imperial shag*

The shags travelled by continuous flapping flight in flock formations low over the sea surface along virtually straight-line flight paths (figure 7). They were registered by radar while making local commuting flights along regular routes between feeding and breeding–roosting areas. Flock size ranged between one (one tracking) and 40 individuals.

Although the shags flew rather fast, they were overtaken from behind by pursuing south polar skuas. Radar tracking of a pair of shags pursued by a skua (figures 7*g* and 8), indicated that the shags in this situation failed to accelerate. Rather, in the case recorded the two shags veered and separated twenty seconds before the pursuing skua dived towards one of them (this dive took place after 150 s, cf. figures 7*g* and 8). After some aggressive turmoil between the shag and skua, the latter soon departed and the shag regained its flight route.

4. DISCUSSION

(*a*) *Observed and predicted speeds*

The power curve for flapping flight (the relationship between power and velocity) and the glide polar for gliding flight (the relationship between rate of sink and forward gliding speed) can be estimated for birds with different body masses and wing morphologies on the basis of flight mechanical theory, according to Pennycuick (1989). From these relationships different significant speeds in flapping and gliding flight can be predicted. In flapping flight the minimum power speed gives the smallest possible energy costs per unit of time, while the maximum range speed is associated with the minimum energy costs per unit of distance covered. In gliding flight the analogous speeds are associated with the minimum rate of sink and with the best glide ratio, respectively. The observed flight speeds of the different seabird species under near-calm conditions are compared with these predicted speeds in figure 9.

For the albatrosses, the giant petrel, great shearwater and antarctic fulmar, the observed flight speeds fall close to the gliding speed giving the best glide ratio, which is somewhat faster than the minimum power speed in flapping flight. Of these species only the albatrosses practised almost pure gliding flight (swell soaring), while the other species proceeded by flap-gliding (some of the yellow-nosed albatrosses also

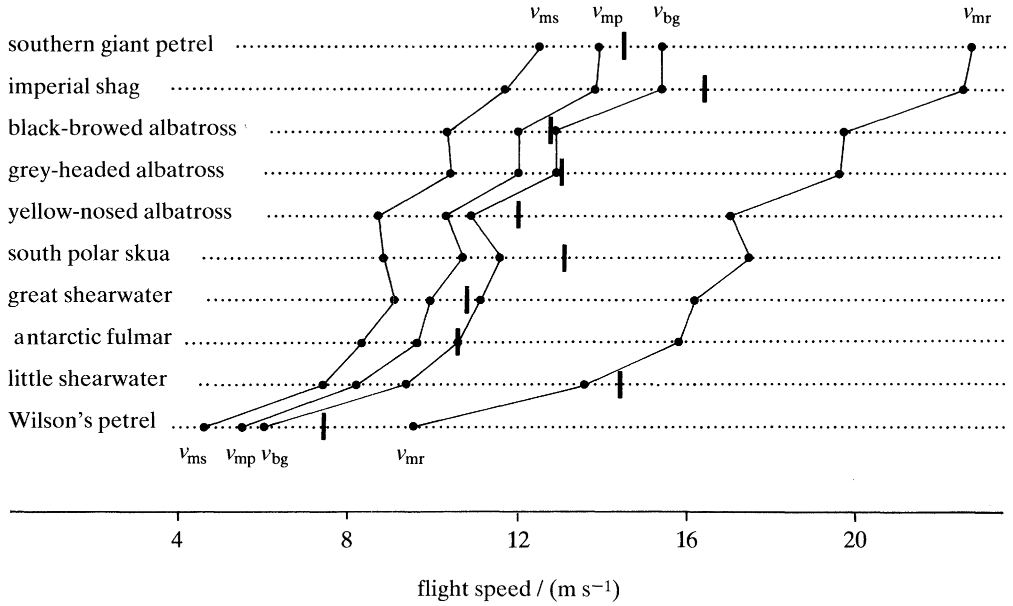

Figure 9. Observed airspeeds of flying seabirds tracked by radar under near-calm conditions, in relation to significant speeds in flapping and gliding flight as calculated from Pennycuick (1989, Program 1 and 2). v_{ms} = gliding speed for minimum rate of sink (coinciding with the estimated stalling speed for most of the species), v_{bg} = gliding speed for best glide ratio, v_{mp} = minimum power speed in flapping flight, v_{mr} = maximum range speed in flapping flight.

used flap-gliding flight). For flap-gliding to be efficient, it may require the bird to adjust its flapping speed towards the speed for the best glide ratio in gliding flight (Pennycuick 1987).

Presumably the flap-gliding birds gain some extra energy from rising air low over the waves and swells not only during the gliding but also during the flapping phases. This will have the effect of shifting the power curve towards lower power levels, and the maximum range speed will be slower than calculated in figure 9. Furthermore, by flying at a low altitude over the sea surface, the birds may benefit from the ground effect giving a reduction in the induced drag (Withers & Timko 1977; Blake 1983, 1985). As a consequence, both the power curve and glide polar will become affected, with predicted significant speeds falling below these calculated in figure 9.

For the remaining four species in figure 9, i.e. the imperial shag, south polar skua, little shearwater and Wilson's storm-petrel, the radar registrations refer to virtually continuous flapping flight. Only the little shearwater travelled at a speed close to the predicted maximum range speed, while the other three species flew at speeds intermediate between the minimum power and maximum range speeds. The shags were tracked while commuting between feeding and breeding–roosting areas, when one would have thought that they should benefit by flying close to or even faster than the maximum range speed (Norberg 1981). Surprisingly slow airspeeds, well below the maximum range speed, have been reported by Pennycuick (1987) also for the closely related and similar-sized shag *Phalacrocorax aristotelis*. One possible explanation suggested by Pennycuick for these slow speeds, is that the shags lack sufficient muscle power to fly as fast as the maximum range speed. The failure of the imperial shags to accelerate when pursued by a south polar skua (figure 8), indeed indicates that the shags may be unable to mobilize much extra muscle power in addition to that expended at their relatively slow normal cruising speeds.

In comparison, the south polar skuas no doubt had the muscle capacity to fly faster than they normally did and to reach their maximum range speed (figure 8). Still, only two out of 22 south polar skuas tracked by radar, and only five out of 27 registered optically, travelled with airspeeds greater than 16 m s^{-1}, i.e. rather close to their predicted maximum range speed. Many of the skuas were clearly looking out for prey while flying, and optimal speeds in foraging flights are unlikely to coincide with either the minimum power or maximum range speed, as will be discussed below.

The airspeed distribution was bimodal for Wilson's storm-petrel depending on whether the birds were foraging while travelling or not (figure 6). During the foraging flights, mean airspeed was close to the minimum power speed, while it approached the maximum range speed on the non-foraging flights. However, there is no general expectation that birds travelling within or between food patches should fly close to the minimum power and maximum range sped, respectively (see below). The storm-petrels tracked by radar while foraging were picking food objects from a smooth sea surface both while in flight, briefly hovering by active wing beats (see Withers (1979) about hovering of this petrel under calm conditions), and while settling on the water for a few seconds.

The maximum range speed is not constant but depends on the wind. To keep energy costs per unit of ground distance covered at the minimum level, birds are expected to increase their airspeed when flying into headwinds and reduce it when flying with tailwinds, as explained by Pennycuick (1978). A negative relationship between airspeed and speed increment caused by wind is to be expected not only for the maximum range speed but also for optimal flight speeds associated with foraging (cf. below). The seabirds travelling by flapping or flap-gliding flight changed their airspeed in accordance with this prediction (table 5). A similar wind effect was found by Pennycuick (1982, 1987) for a larger number of seabird species, some of which were the same as in this study.

For birds proceeding by pure gliding and soaring, the rate of energy expenditure (i.e. muscle power required for holding the wings in gliding position and maintenance power) is independent of the airspeed. Hence, to minimize energy costs over distance it should pay to travel at the maximum possible resulting airspeed in all wind conditions. A negative relationship between airspeed and speed increment caused by wind is expected only if headwind conditions permit the birds to obtain faster travelling speeds in relation to the surrounding air than are obtainable under tailwind conditions. We found no correlation between mean airspeed over longer distances (1–5 km) and wind for the gliding and soaring albatrosses (table 5), while such a correlation was demonstrated by Pennycuick (1982) for shorter segments (some hundred metres) of gliding flights.

(*b*) *Optimal speeds on foraging flights*

Most of the south polar skuas and Wilson's storm-petrels were tracked while on foraging flights, searching for and gathering food as they travelled. Food searching may well have occurred also during the flights of some of the other seabirds. This induces us to briefly and schematically consider what are the optimal speeds to be expected on foraging flights. General conditions for optimal travel speeds by foraging animals have been evaluated and reviewed more extensively by Pyke (1981) and Houston (1986, 1992).

A foraging bird may be expected to maximize its resulting (net) energy gain (R) which is the difference between the energy intake rate (E) and the power expenditure (P) during flight: $R = E - P$. Both E and P are functions of the flight speed (v), and in flapping flight $P = f(v)$ according to the power curve mentioned above. Consequently, maximum R is associated with the condition $\mathrm{d}E/\mathrm{d}v = \mathrm{d}P/\mathrm{d}v$. The energy intake function $E = f(v)$ may take on different forms, and one general and three special cases are illustrated in figure 10.

In the general case, the energy intake rate is expected to increase initially with flight speed as the bird encounters an increased amount of prey per unit of time the faster it covers ground. However, searching will become progressively less efficient the faster the bird goes, and the energy intake rate will level off and fall at fast speeds, where the probability of prey detection drops to low levels. The optimal foraging flight speed associated with $R_{\max}$ is illustrated in figure 10*a*.

The optimal foraging speed will always fall between the flight speeds for $E_{\max}$ and $P_{\min}$, respectively. It will be below the minimum power speed if prey is very difficult to detect and E reaches its maximum already at speeds lower than the minimum power speed (cf. Gendron & Staddon (1983, 1984) about cryptic prey). It will be faster than the minimum power speed if the speed associated with $E_{\max}$ falls above the minimum power speed or if E is a monotonically increasing function of v. The optimal foraging speed is expected to increase with prey availability (increased steepness of E-curve; ignoring take-off costs, cf. Houston (1986)). Furthermore, the optimal airspeed depends

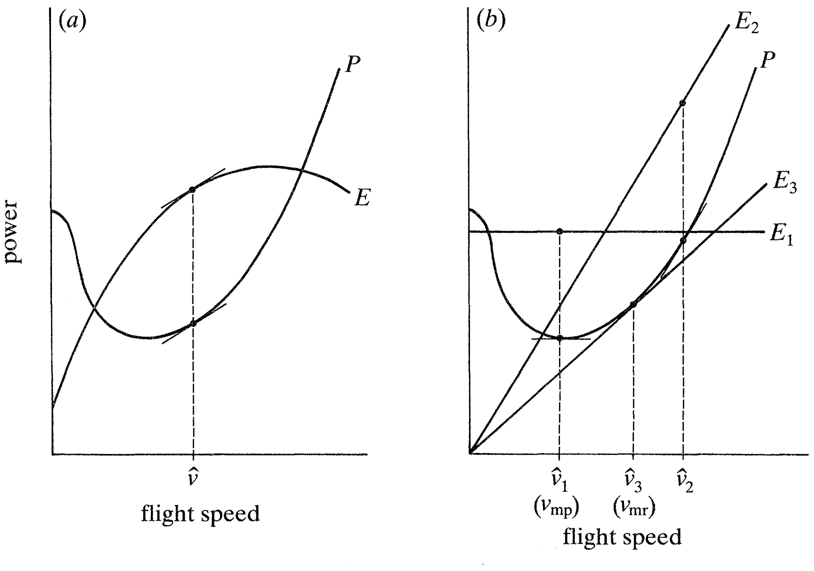

Figure 10. Optimal speeds for birds on foraging flights (see text). P represents the power curve for flapping flight and E is the energy intake rate plotted in relation to flight speed. (*a*) Optimal foraging speed for a general case. (*b*) Optimal foraging speeds for three special cases of relationship between E and flight speed. In cases 1 and 3 the optimal speed coincides with the minimum power speed (v_{mp}) and maximum range speed (v_{mr}), respectively.

on wind, being faster in headwinds than in tailwinds. This arises as a consequence of the fact that E is a function of the groundspeed whereas P is a function of the airspeed. The effect of wind can be taken into account by shifting the E-curve in figure 10*a* to the left or right by the amount of speed increment caused by tail- or headwinds, respectively.

The south polar skuas changed their airspeed in relation to wind as expected, whereas the Wilson's storm-petrels were recorded under a too narrow range of wind conditions to permit analysis of this aspect. It will be noticed that without knowing the relationship between E and v for birds on foraging flights, their specific optimal flight speeds cannot be predicted.

If energy intake rate is independent of the foraging flight speed (e.g. prey detected or available through movement of its own), as in case 1 in figure 10*b*, the minimum power speed is optimal (unless look-out posts are available which would make a 'sit-and-wait' behaviour the best option). Such a situation may apply to the foraging Wilson's storm-petrels which flew close to the minimum power speed. Another contributory cause of the slow flight speed of this species may be the costs for accelerating to the preferred flight speed after each stop for food picking. With a high frequency of feeding stops (according to our rough estimation the foraging storm-petrels made food picking stops on average every 40 s and 200 m), such take-off costs will act to significantly reduce the optimal speed as evaluated by Houston (1986).

If energy intake rate increases linearly with flight speed as in case 2 in figure 10*b* (e.g. conspicuous and stationary prey), the optimal speed will exceed the maximum range speed as long as there is a positive net energy gain. Only if energy intake and expenditure balance will the maximum range speed be optimal (case 3 in figure 10*b*). Airspeeds faster than the maximum range speed are expected also when birds fly between well-defined food patches (without searching and foraging during the between-patch flights). With increasing distance between the food patches, the optimal flight speed becomes reduced, approaching the maximum range speed. Flight speeds exceeding the maximum range speed are also expected for birds transporting food to their young (Norberg 1981) and for birds completing their migratory journey as fast as possible (Alerstam & Lindström 1990).

The above considerations illustrate the difficulties of interpreting observed speeds during foraging flights in relation to the minimum power and maximum range speeds. For many marine birds the preferred flight speeds during food searching seem to be intermediate between these two characteristic speeds. This has been reported for several species of gulls and terns flying in the vicinity of their breeding colonies (Schnell & Hellack 1979) and applies also to the south polar skua and the Wilson's storm-petrel in this study.

(*c*) *Resulting travelling speed and flight economy*

The albatrosses show the greatest propensity and diligency among seabirds to exploit energy from the wind over the sea surface. By practising both static (wave and swell soaring) and dynamic soaring they habitually travel by pure gliding flight. The principles for their soaring flights have been treated extensively (Idrac 1924; Cone 1964; Wood 1973; Wilson 1975; Pennycuick 1982), but the complexity of the behaviour makes it difficult to predict theoretically resulting travel speeds under different wind conditions. Our data provide useful information about the albatrosses' performance in this respect (figure 11).

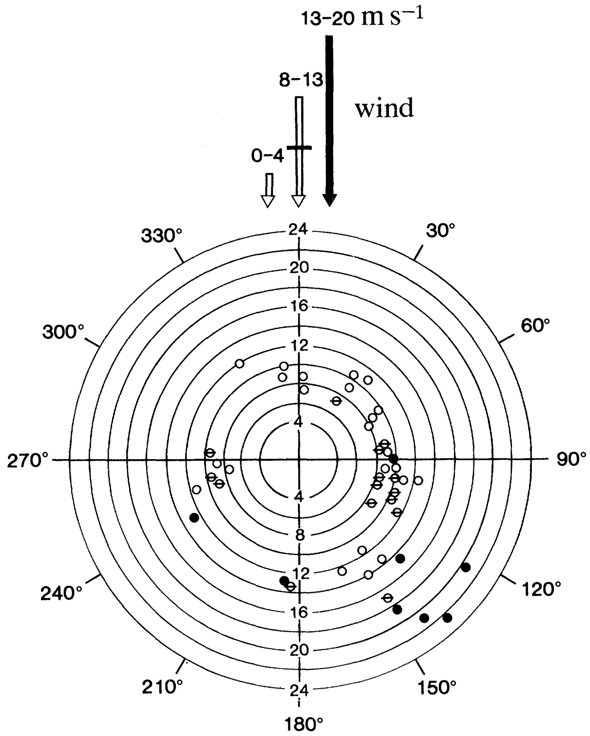

Figure 11. Resulting speed and direction of travel of albatrosses in relation to the wind direction. Different symbols refer to flights in weak, moderate and strong winds, as indicated. Of the 46 cases plotted, 23 refer to black-browed, 11 to grey-headed and 12 to yellow-nosed albatrosses.

The resulting travel speed was determined as the straight-line distance from initial to final position divided by the total time for each of our trackings (i.e. groundspeed multiplied by straightness in tables 3 and 4). In weak winds (less than 4 m s^{-1}) the albatrosses travelled in various directions relative to the wind with a mean resulting speed of 10.3 m s^{-1} (s.d. = 2.0 m s^{-1}, $n = 23$). With moderate winds the average speed remained the same (10.2 m s^{-1}, s.d. = 2.6 m s^{-1}, $n = 15$) but the birds now mostly travelled almost at right angles to the wind (median angle = 104° to the left–right of the wind). In stronger winds (13–20 m s^{-1}) the albatrosses travelled faster, with a mean resulting speed of 16.6 m s^{-1} (s.d. = 4.7 m s^{-1}, $n = 8$), mostly in oblique following winds (median angle = 136° left–right of the wind). The albatrosses seemed to avoid heading into moderate or strong opposed winds, possibly because they cannot cover ground efficiently in this direction by their soaring flight technique. Their flight technique may also make it difficult for them to take full advantage of the tailwind force and to reach high speeds when travelling due downwind (cf. figure 2*g*).

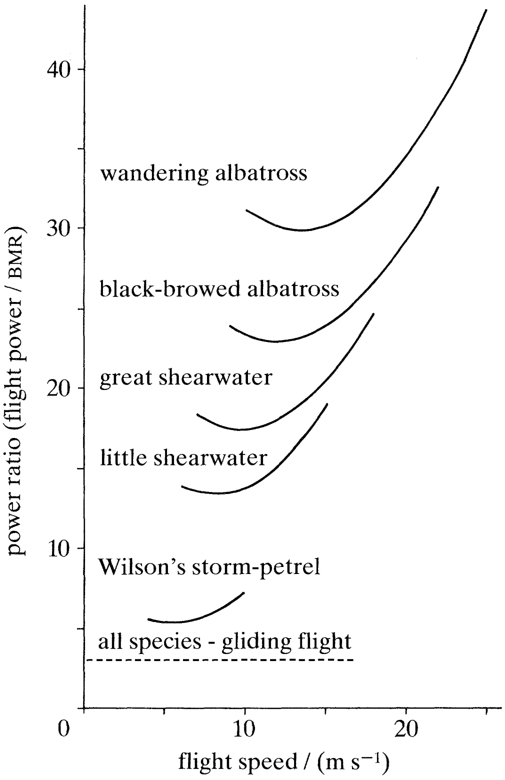

Figure 12. Flight power relative to the basal metabolic rate (BMR) for seabirds of different sizes as estimated for an intermediary range of flapping flight speeds (including the minimum power and maximum range speeds) according to Pennycuick (1989, Program 1). Power expenditure during gliding flight is about 3 × BMR for all species independently of size and speed. Resulting travel speeds in gliding–soaring flight depends on environmental conditions as well as on the gliding characteristics of the different species.

We recorded three cases of resulting groundspeed above 20 $m\ s^{-1}$ with a maximum at 22.5 $m\ s^{-1}$ (figure 11). The smaller albatross species tracked in our study seem to perform almost as well as the large wandering albatross, as judged from recent reports of travelling speeds of this species based on satellite telemetry (Jouventin & Weimerskirch 1990; Prince *et al.* 1992). Maximum travel speeds of wandering albatrosses ranging widely over the ocean were between 17.4 and 24.5 $m\ s^{-1}$. Over longer distances (between 400 and 1000 km) they reached average ground speeds of 14–16 $m\ s^{-1}$ under windy conditions, although their overall round-trip speeds (including foraging) were much slower.

The energy cost during gliding flight of wandering albatrosses has been estimated by Adams *et al.* (1986) to be about three times the basal metabolic rate (BMR calculated from the allometric equation given by Lasiewski & Dawson (1967)). There are good reasons to assume that gliding flight power amounts to approximately the same multiple of BMR for most bird species (Adams *et al.* 1986; Pennycuick 1989). If the albatrosses were to travel by flapping flight, their power expenditure would be much higher, 22–35 times BMR (figure 12). The flapping flight power as a multiple of BMR is expected to increase with the birds' body mass for reasons explained by Pennycuick (1989).

Comparing albatross soaring–gliding and flapping flight by their associated costs of transport (energy cost per unit of distance covered, i.e. the flight power divided by the resulting travel speed), shows that even with very slow resulting speeds, soaring flight will be by far most favourable (figure 12). Only when the resulting progress by soaring flight in neutral winds is as slow as 2 $m\ s^{-1}$, is the cost of transport by gliding and flapping flight approximately equal. In flapping flight, birds can make full use of the tailwind assistance while travelling due downwind. For soaring flight to be preferable over flapping flight (lower cost of transport) in strong tailwinds, say 20 $m\ s^{-1}$, the albatrosses must be able to glide at resulting speeds exceeding 4 $m\ s^{-1}$. Even if they are inefficient in utilizing the potential wind assistance in downwind soaring flight (figures 2*g* and 11), they do much better than this and can still save much energy by their soaring flight technique.

Procellariiform seabirds resort to flapping flight to an increasing degree (mostly mixed with gliding in a flap-gliding technique) the smaller they are. This may be expected for two reasons: (i) energy expenditure in flapping flight relative to that in gliding flight decreases with decreasing body size (figure 12); and (ii) the smaller species will be less capable of efficient progress by sustained gliding flight in static as well as dynamic soaring (Cone 1964; Wilson 1975; Pennycuick 1982).

(*d*) *Flight pattern and wind*

From figure 11 is seen that the albatrosses travelled more often with winds from their left than from their right side. The preponderance for left-wind flights is similar (three out of four cases) under weak, moderate as well as strong winds. This pattern, based on 46 trackings from 10 different days, is suggestive, although statistical inferences cannot be drawn because the trackings hardly satisfy critical criteria for independence (if so, the pattern would have been highly significant according to the binomial test).

In the southern hemisphere travelling with winds from the left side would lead the birds away from low pressure centres and towards high pressure cells and ridges. This is contrary to the expected flight pattern according to Jouventin & Weimerskirch (1990). They found that wandering albatrosses with satellite transmitters made very limited movements near high pressure areas, perhaps as a consequence of the low wind speeds and thus less favourable conditions for efficient soaring flight progress. Hence they concluded that 'high-pressure systems acted as traps that could immobilize the birds for periods of 1–7 days'. However, our observations raise the possibility of quite another speculative interpretation: that the high pressure areas offer the best conditions for efficient foraging and that this is the reason why the albatrosses go there (travelling with winds from their left) and stay there for some time. According to this view, the high pressure areas may be regarded as ephemeral and moving food patches for the albatrosses. Blomqvist & Peterz (1984) analysed pelagic seabird movements and proposed that seabirds in the northern hemisphere may fly with the wind mainly from their right side, thereby avoiding depressions and weather conditions unfavourable for foraging. Abrams *et al.* (1981) found that the oceanic distribution of wandering albatrosses was not significantly different from random in relation to the wind strength.

The wind sets bounds to the operational possibilities of the seabirds, but it also serves the birds well in their economic gliding and flap-gliding flight techniques. Although the flight paths on a finer scale are at times winding and complex, over longer distances the seabirds make progress on remarkably consistent courses and with fair travel speeds, as demonstrated in this study. However, much remains to be discovered about the fascinating interplay on a wider scale between weather systems and seabird movements over the open ocean, as well as on a finer scale between the motions of winds, waves and seabirds.

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