THE ROYAL SOCIETY

doi 10.1098/rspb.2000.1223

Fast and fuel efficient? Optimal use of wind by flying albatrosses

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The influence of wind patterns on behaviour and effort of free-ranging male wandering albatrosses (*Diomedea exulans*) was studied with miniaturized external heart-rate recorders in conjunction with satellite transmitters and activity recorders. Heart rate was used as an instantaneous index of energy expenditure. When cruising with favourable tail or side winds, wandering albatrosses can achieve high flight speeds while expending little more energy than birds resting on land. In contrast, heart rate increases concomitantly with increasing head winds, and flight speeds decrease. Our results show that effort is greatest when albatrosses take off from or land on the water. On a larger scale, we show that in order for birds to have the highest probability of experiencing favourable winds, wandering albatrosses use predictable weather systems to engage in a stereotypical flight pattern of large looping tracks. When heading north, albatrosses fly in anticlockwise loops, and to the south, movements are in a clockwise direction. Thus, the capacity to integrate instantaneous eco-physiological measures with records of large-scale flight and wind patterns allows us to understand better the complex interplay between the evolution of morphological, physiological and behavioural adaptations of albatrosses in the windiest place on earth.

Keywords: heart rate; Southern Ocean; wandering albatross; flight patterns

1. INTRODUCTION

Wandering albatrosses forage at extensive distances from their nests in the Southern Ocean (Jouventin & Weimerskirch 1990; Weimerskirch 1998), relying on prey that are widely dispersed and encountered irregularly throughout their foraging trips (Weimerskirch *et al.* 1994; Viswanathan *et al.* 1996). Remarkably, the overall energy expenditure (EE) while foraging, measured with doubly labelled water, is very low (Adams *et al.* 1986; Arnould *et al.* 1996) and wandering albatrosses have a low ratio of $EE_{foraging}/EE_{resting}$ compared to other species of birds and mammals (Daan *et al.* 1990; Hammond & Diamond 1997). Flight energetic models suggest that low costs could be achieved by the use of dynamic soaring where birds take advantage of wind conditions (Cone 1964; Wood 1973; Pennycuick 1982, 1989) or increase flight speeds to maximize distance covered (Alerstam *et al.* 1993). The lack of wind has been suggested to increase EE of foraging petrels and albatrosses (Furness & Bryant 1996). Because of their morphology, with long narrow wings and heavy weight, sustained flapping flight would be energetically impossible for wandering albatrosses in the absence of wind (Alerstam *et al.* 1993). Low costs of flight are also assisted by the anatomical adaptation of a tendon wing lock, this being confined among large gliding birds to albatrosses and giant petrels (Pennycuick 1982). Alternatively a reduced-flight activity when at sea, i.e. long periods sitting on the water, may explain overall low costs but would also reduce time and distance foraged and therefore the probability of encountering prey since prey are detected in flight (Weimerskirch *et al.* 1997). Low foraging costs are probably critical to the unique life-history pattern of albatrosses (Costa 1991) and especially so in reducing the time and energy constraints imposed on central-place foragers by distant foraging (Ydenberg *et al.* 1992). However, the reliance on wind to reduce foraging costs was impossible to prove in the absence of a metric that can be linked to effort exerted during different phases of foraging flight over the open sea. To be able to demonstrate how wind affects foraging costs it is necessary to obtain a precise time–energy budget and therefore estimate EE and effort in relation to the different activities at sea and to wind conditions. Previous studies have shown that heart rate offers a convenient measure of instantaneous effort and EE (Bevan *et al.* 1994, 1995). We use this technique in addition to miniaturized units measuring the exact timing of activity and location in the open ocean to examine how the wind pattern affects costs of foraging and flight patterns during foraging bouts. In a second step we analyse the patterns of movements of satellite-tracked birds to examine on a much larger scale whether wandering albatrosses can consistently take advantage of wind conditions when they depart on a foraging trip.

2. METHODS

The study was carried out on Possession Island, Crozet Islands, Southern Indian Ocean, in January–March 1999. Seven male wandering albatrosses were each fitted with three miniaturized electronic devices (total mass 80 g): a heart-rate transmitter–recorder, an activity recorder and a satellite transmitter; the total mass of the three electronic systems representing only 0.75% of the mass of male albatrosses. Heart rate was measured using an external heart-rate recorder–transmitter (PE4000, Polar, Elektro Oy, Kempele, Finland) coupled with a receiver-logging system (Vantage NV watches, Polar). Electrodes were made of gold-plated safety pins placed under the skin. Heart rates were measured every 60 s over five days during each foraging trip at sea. The two heart-rate loggers (40 g) were taped on the back feathers. The activity of the bird was recorded through

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Received 19 April 2000 *Accepted* 2 June 2000

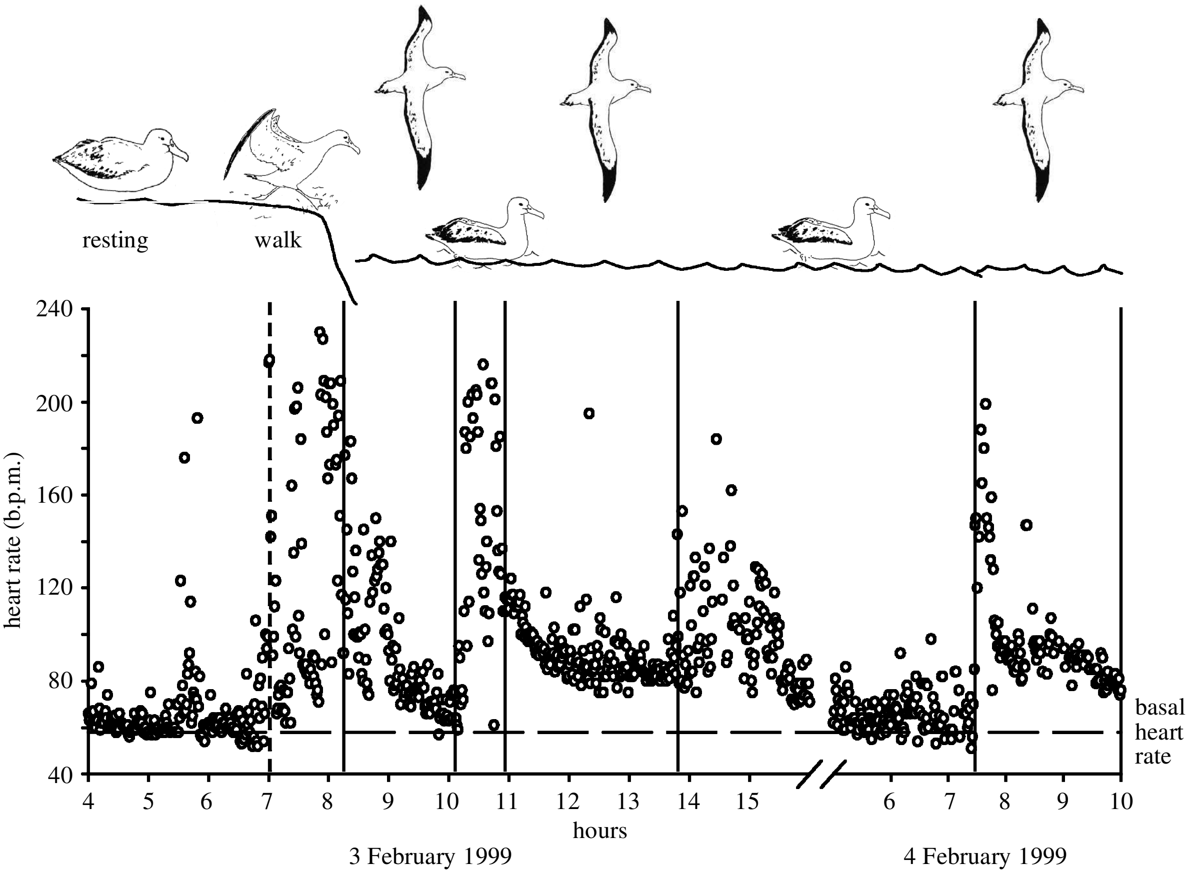

Figure 1. Heart rate of a male wandering albatross recorded during 15 h on 3–4 February 1999. The bird was engaged in various activities on land (sitting and walking) and at sea. When at sea, the exact timings of take-offs or landings recorded by the activity recorder (see § 2) are indicated by the plain vertical bars. The dashed horizontal line indicates the basal heart rate for the bird resting on land. When sitting on the water at 6–7 h of the second day, or when in flight at 9–10 h of the first day, the heart rate reached values close to basal levels.

direct observation when the bird was on land and derived from an activity recorder when the bird was at sea. The activity pattern (sitting on water or in flight) was measured with an activity recorder (20 g, Francis Instrument, Cambridge, UK) that recorded every 15 s whether it was submerged in seawater or in the air. The activity recorder was fitted onto the tarsus using a plastic leg band. When in flight, birds tuck their legs in the plumage (dry) and when on the water, the legs are submerged. Each bird was also fitted with a 20 g Microwave 100 (Microwave Telemetry, Columbia, MD, USA) satellite transmitter (Plateform Terminal Transmitter, PTT) that was taped onto the back feathers using adhesive tape. The PTT provided the position of the bird every 1.5 h on average through the Argos System (CLS Argos, Toulouse, France). Analysis of satellite fixes was performed using ELSA software (CLS Argos, Toulouse, France) after data were filtered according to procedures described in Weimerskirch *et al.* (1993). The activity pattern and flight speed were estimated using satellite fixes and activity recorders. Wind direction all along the route taken by the bird was calculated using the route direction and the direction of the wind derived from meteorological models estimating twice daily the wind strength and wind direction in the southern hemisphere (Météo-France, Toulouse, France). All data (heart rate, activity, position, bathymetry, meteorology) were estimated every minute using authors' own software (Diomedea 15.0) that integrates all the data and estimates geographic positions every minute based on activity and positioning by the Argos system, as well as flight speed. In addition, 82 foraging trips of breeding wandering albatrosses from Crozet studied by satellite tracking between 1991 and 1999 were used to examine the overall movements of birds.

3. RESULTS

Heart rates were lowest when birds were resting on land (65 beats per minute, b.p.m.) and highest when birds were walking on land, or taking off from land or the sea (230 b.p.m.; figure 1). When in flight, the heart rates of albatrosses were, at times, nearly as low as those of birds resting on land (figure 1). During foraging trips at sea, birds spent on average 51.8 ± 15.9% (range, 33.3–72.9%) of their time sitting on the water, which was when heart rates were at their lowest values. However, sporadic increases in heart rate did occasionally occur when birds were sitting on the water, which were possibly associated with feeding and prey handling, or agonistic behaviour (figure 1). These increases in heart rates could also be associated with ingestion and digestion of prey as this has been shown to increase metabolic rates (Hawkins *et al.* 1997). Albatrosses landed (or took off) on average 15.0 ± 4.5 times per day (range, 7.1–19.4) and during these events elevated heart rates occurred in bursts of 15–20 min. In some cases, heart rates increased just prior to taking off, suggesting that birds experienced an anticipatory response (figures 1 and 2). Average values indicate that the initial tachycardia measured after taking off

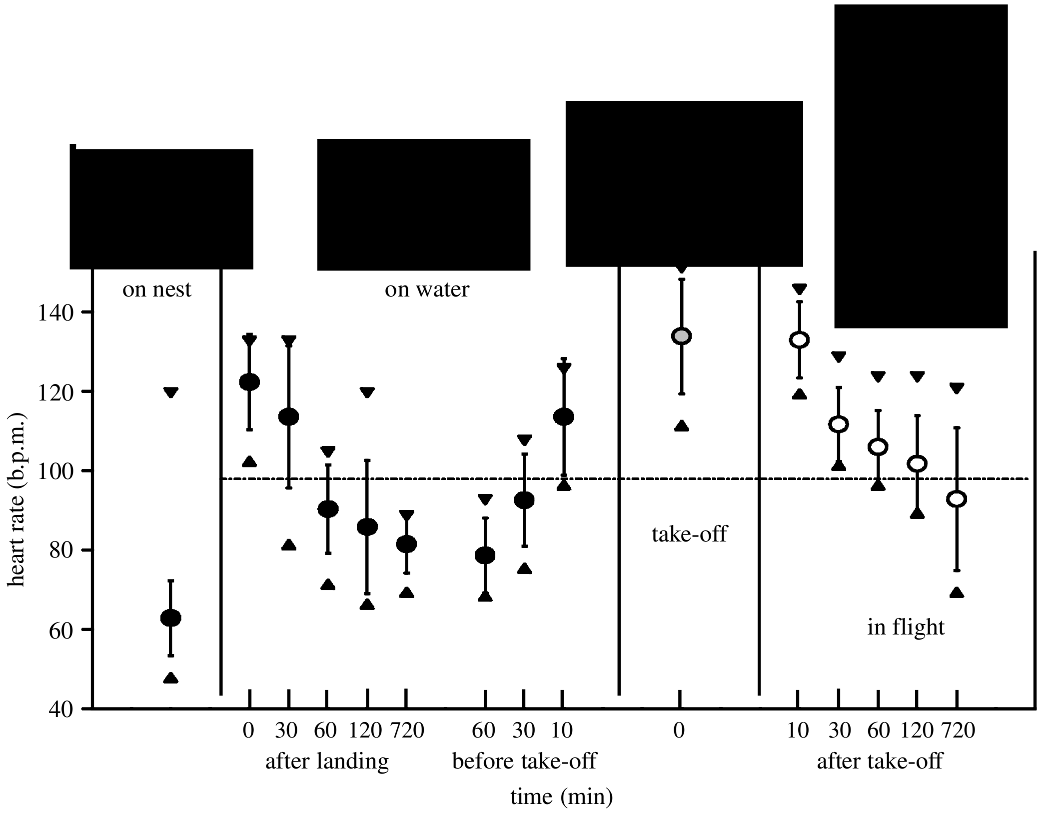

Figure 2. Average heart rates (± s.e.m.) of seven albatrosses resting on the nest, sitting on the water (for different periods of time after landing and before taking off), taking off and in flight (for different periods after taking off). For each activity, we have calculated average values and filled triangles represent the range for each average. Differences between activities were highly significant ($F_{14,6} = 16.8$; $p < 0.01$). The dotted line indicates the average heart rate over the entire measurement period during foraging trips for the seven birds (97.4 ± 5.2 b.p.m.). There is a progressive decrease in heart rate after take-off indicating that prolonged flight does not result in increased costs. A progressive decrease was also apparent for birds landing and resting on the water. Low values on water were attained after long periods on water, which occurred mainly at night when birds were probably sleeping. Surprisingly, before take-off there was a progressive increase in heart rate, indicating an anticipatory response.

decreased progressively during flight for several hours, reaching a minimum value close to that of birds resting on water (figure 2). Overall, albatrosses showed a preference for flying with tail or side winds (figure 3*a*). When we combined our indices of foraging effort with measurements of flight behaviour, the results suggest that albatrosses maintain a low expenditure (i.e. low heart rates) when flying with tail or side winds (figure 3*b*). Surprisingly, albatrosses also achieved the highest flight ground speeds when travelling in these wind conditions (figure 3*c*). In contrast, birds flying into a head wind experienced increases in heart rate at the same time as ground speeds decreased; head winds were encountered in less than 4% of the tracks analysed (figure 3).

The analysis of 82 long foraging trips made by albatrosses breeding on Crozet show that birds exploit an area of 16 million square kilometres, ranging from tropical waters to the Antarctic continent (figure 4, centre). Large-scale movements are covered preferentially with tail and side winds (figure 3) with preference for winds coming from the right (61.3% of bouts with right winds; $\chi^2_1 = 7.35$; $p < 0.01$). Wandering albatrosses forage in a part of the Southern Ocean that experiences some of the strongest and most consistent winds on earth. Meteorological models of wind patterns for this area averaged over the past four years indicate that wind patterns are seasonably predictable (figure 4, centre). Thus, when heading to sea, albatrosses breeding on Crozet experience a regular west by north-west wind flow of the roaring forties, which facilitates travel to the east, north or south of the island. When departing on long foraging trips, satellite-tracked birds indeed fly either north-east or south-east preferentially. They fly a stereotypical looping course with striking regularity (figure 4, right), either clockwise when heading south, or anticlockwise when heading north. Birds conducting shorter journeys at the same latitude as Crozet tend to use a figure-of-eight-type movement.

4. DISCUSSION

The first major result of this study shows that albatrosses cruising with favourable winds can achieve very low flight costs. Although it has been previously suggested that foraging energy costs of wandering albatrosses are overall low, we show here that these costs are mainly due to extremely low costs of the flight itself. In some circumstances, heart rates during flight were close to basal levels, whereas previous studies suggest that gliding flight incurs a cost of about three times the standard metabolic rate (Baudinette & Schmidt-Nielsen 1974; Hedenström 1993). Remarkably, wandering albatrosses attained the

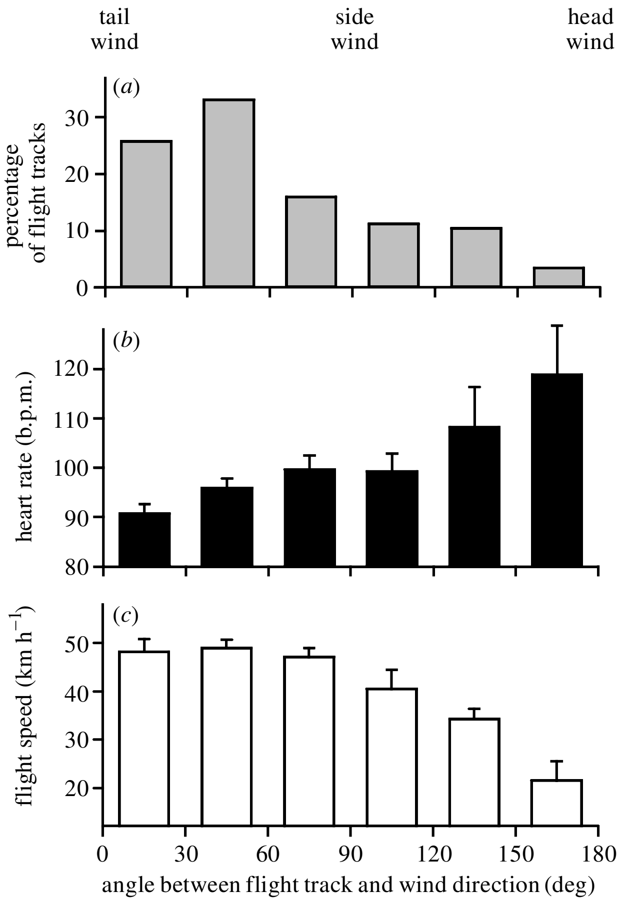

Figure 3. (*a*) Percentage of flight tracks between locations where albatrosses were flying with various wind conditions, indicating that birds preferentially fly with tail to side winds ($\chi^2_5 = 33.7$; $p < 0.001$). (*b*) Heart rates (measured at least 30 min after a take-off) varied according to the angle between the wind direction and the flight direction ($F_{5,6} = 7.5$, $p = 0.015$); they increase when birds fly from tail to head winds. (*c*) Flight speeds also varied according to wind ($F_{5,6} = 10.4$, $p = 0.006$) but decreased when birds fly from tail to head winds.

lowest effort in flight when flight ground speeds were highest, demonstrating the true economy of soaring flight in birds. Travelling with favourable winds for long periods appears to require little effort compared to landing and taking off, as indicated by our measures of heart rate. Since albatrosses mainly fly with favourable winds and land relatively infrequently, the low overall EE compared to other birds and mammals (Daan *et al.* 1990; Hammond & Diamond 1997) is paradoxically likely to be more influenced by behaviour on the water (landings and take-offs, or prey handling) than by actual flight costs or distance travelled.

The flight behaviour of albatrosses studied at sea by ship-based observers shows that birds engage in a variety of manoeuvres while soaring (figure 4*a*); however, they preferentially fly with side winds blowing from the left (Alerstam *et al.* 1993). The frequent turns, pull-ups and descents typical of zigzag flight on a small scale are integrated by the bird into medium-scale movements as studied remotely with satellite tracking (figure 4*b*), which is when our estimates of time–energy budgets were obtained. Our results indicate that at this scale birds appear to favour winds coming from the right. In the Southern Ocean, travelling preferentially with winds from the right would direct birds away from high-pressure cells, where wind strength is weakest in the centre of the high. The reason why at a small scale birds tend to fly with winds coming from the left (Alerstam *et al.* 1993) is not clear. The medium-scale movements are then integrated into large-scale movements with a consistent overall orientation in smooth loops or with a twisted shape as shown by satellite tracks (Jouventin & Weimerskirch 1990; Weimerskirch *et al.* 1997) (figure 4*c*). Wandering albatrosses are central-place foragers during breeding, always returning to a central starting point, while flying with favourable winds, raising the question of how they can maintain a consistent overall trajectory when wind conditions change continuously with the permanent merry-go-round oscillations in pressure systems of the Southern Ocean. This question is probably less crucial when birds are not breeding (Nicholls *et al.* 1997; Weimerskirch & Wilson 2000). Our results indicate that albatrosses do not wander aimlessly across the Southern Ocean but appear to travel in flyways that provide favourable winds throughout their foraging trip. The use of stereotypical movements (clockwise or anti-clockwise) allows birds at the extreme south and north parts of the range to use the prevailing easterly flow to move westward without a head wind (figure 4, centre). This pattern of prevailing winds also shows that winds directly to the east or west of Crozet would be the least favourable because of the strong west-to-east flow. Thus, birds conducting short journeys at the same latitude as Crozet (e.g. during chick brooding) experience strong head winds either as they depart heading west or upon returning from the leeward side of the island. Consequently, albatrosses tend to use a figure-of-eight-type movement, which is similar to the 'tacking' movements used by sailboats.

The reason why flight costs increase with head winds requires additional studies. It could be due to the fact that birds include flapping into their soaring flight to a higher degree in head winds, because they have to make tacks continuously. As a result flight speed decreases with increasing head winds. Because winds are predictable in this area, the largest albatrosses can rely on a foraging strategy that is based on high-speed travel at a low cost of flight to cover extremely large areas in search of prey. It is a strategy, which is probably compulsory for such a large species, for which wind consistency is crucial for flight. It explains why today large albatrosses are restricted to this part of the Southern Ocean where winds are the most consistent and powerful. Smaller species of albatross are probably not so constrained by wind conditions and are indeed found in more diverse oceanic environments. The reliance on wind and the tendency to use preferential flight directions according to wind directions suggest that when leaving breeding grounds, wind direction could be the main factor that determines flight direction and possibly foraging zones.

Several analyses of bird movements have shown them to be adapted to large-scale predictable wind patterns associated with low-pressure systems and latitudinal wind and pressure zones on earth (e.g. Lack 1953; Alerstam 1981; Blomqvist & Peterz 1984). These studies concern

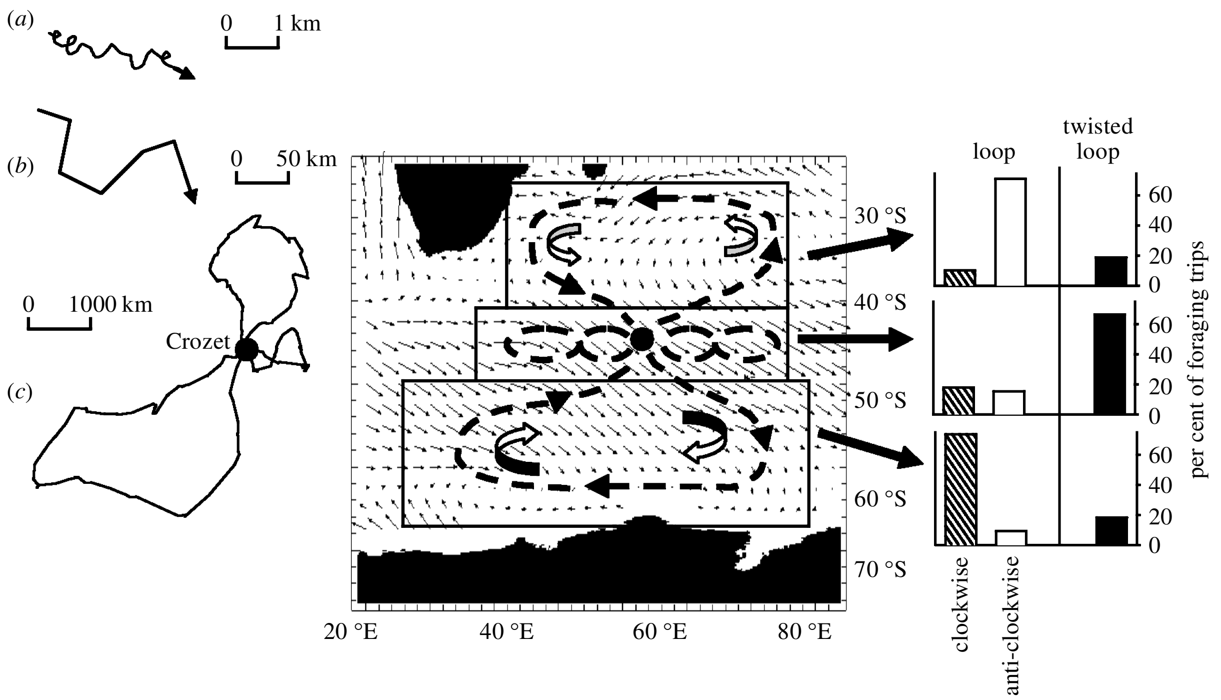

Figure 4. Left, movements of wandering albatrosses viewed at different scales: (*a*) small-scale movement as reconstructed from ship-based observations (Pennycuick 1989; Alertsam *et al.* 1993); (*b*) medium-scale movement as reconstructed from satellite tracking; (*c*) large-scale showing three entire round trips from the Crozet islands. Centre: map of the south-western Indian Ocean with the monthly average wind directions (arrows) and strengths (dependent on the lengths of the arrows) in February 1999 (source IGOSS; surface winds calculated using boundary-layer similarity theory: Marine Weather Service Office, Bureau of Meteorology Melbourne, http://ingrid.ldgo.columbia.edu/SOURCES/IGOSS/Australia). The data indicate that average monthly wind strengths and wind directions in January and February of 1996–1999 were very similar, suggesting that wind patterns are very predictable. The Crozet islands are indicated by the black dot in the centre of the map. Wandering albatrosses forage over an area of 16 million square kilometres as indicated by the cumulative total area of the three boxes. The general flyways taken by birds foraging to the north, to the south or at similar latitudes to Crozet are indicated by the dashed lines and the direction of flyways denoted by the arrows. Right, when foraging at similar latitudes to Crozet (range ± 2° latitude), flight patterns mainly have a twisted shape, whereas when foraging at higher or lower latitudes, trips have a circular path ($\chi_1^2 = 18.8$; $p < 0.001$). Flights north of the island are typically in an anticlockwise direction whereas when foraging to the south, most flights are in a clockwise direction ($\chi_1^2 = 17.8; p < 0.001$).

mainly migratory birds. Large-scale anticlockwise or clockwise movements are known to occur in some species (e.g. Curry-Lindhal 1982; Marshall & Serventy 1965). However, the role of wind in shaping the evolution of an optimal foraging route is still an open field of research (Liechti & Bruderer 1998), especially for birds foraging during the breeding season. At this time, breeding requirements put additional and severe constraints on optimal foraging strategies. Our results suggest that the use of wind by albatrosses has led to the selection of an extreme flight strategy that could only have evolved in the windiest place on earth. The changes in wind regime and variability that are predicted to occur with future changes in the world climate (Intergovernmental Panel on Climate Change 1995) may inevitably impair the foraging ability of a species relying so closely on predictable wind conditions. This could be an additional unexpected biological consequence of global changes.

This study was supported by Institut Français pour la Recherche et la Technologie Polaire, by NSF–CNRS and National Geographic Research grants. We thank Y. Cherel, Y. Handrich, R. P. Wilson and two anonymous referees for helpful comments on the manuscript.

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