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Movements in Adélie penguins foraging for chicks at Ardley Island, Antarctica; circles within spirals, wheels within wheels

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Abstract: Eighteen Adélie penguins *Pygoscelis adeliae* tending chicks at Ardley Island (62° 13' S, 58° 55' W), Antarctica during December 1991 and January 1992 were equipped with multiple channel data loggers recording swim heading, speed and dive depth. These parameters were then equated together using vectors to calculate the foraging tracks of the birds at sea as well as depth utilisation. The deepest dive recorded was 97 m although most dives terminated within 70 m. In accordance with previous studies, descent and ascent speed of diving birds increased with maximum dive depth and absolute time spent for the descent and ascent increased with maximum dive depth. The distance moved to the farthest point from the island was 35 km although 70% of all time at sea was spent within 10 km of the island (all birds considered together). Consideration of the fine scale features of bird movement indicated that three major patterns were apparent; (i) virtual straight line movement, (ii) a circular or spiralling movement where circles had diameters ranging between 20 and 200 m and (iii) extensive movement without any substantial displacement. A travel index (total distance travelled during a specified time divided by the straight line distance covered during this time) showed that the three behaviours had very different values. The frequency of occurrence of particular travel index values followed a logarithmic decay with straight line travel (with indices around 1) accounting for *ca.* 35% of all movement at sea with greater deviations from a straight line course occurring less often. It is supposed that straight line travel serves displacement, highly localised movement reflects prey pursuit and that the circular or spiralling movement arises from birds seeking out prey using detection systems other than vision.

key words: Adélie penguin, *Pygoscelis adeliae*, movement, diving, foraging tracks

Introduction

The Adélie penguin *Pygoscelis adeliae* is a major top predator in the Antarctic with a circumpolar distribution and a population numbering some 15 million birds (Williams, 1995 and references therein). This bird feeds primarily on euphausiid crustaceans which it catches by pursuit diving to depths of up to 180 m (Williams, 1995; Whitehead, 1989). Since a single Adélie penguin is reported to have to consume between *ca.* 500 and 1200 g food per day, depending on breeding status (Culik, 1993), it is clear that this species may have a substantial, at least local, impact on prey stocks, particularly since, during the breeding season movement is restricted. The areas used for foraging during breeding around a colony (*cf.* Sadleir and Lay, 1990; Davis *et al.*, 1988; Kerry *et al.*, 1995) would appear to depend primarily on the speed at which birds can travel and the time

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they can spend away from the nest (*e.g.* Lishman, 1985). However, this approach was shown to overestimate foraging ranges since few, if any, birds swim a straight line course (Wilson *et al.*, 1989b). Finally, it became clear that the actual areas prospected by foraging penguins depended critically on the manner that birds actually searched. Random walk searching, for example, would only lead to slow departure from the colony (Larralde *et al.*, 1992) while highly directional travel has the reverse effect. The degree to which penguins engage in particular types of travel, therefore, determines the areas available to them for foraging.

The work presented here looks at the space utilisation of Adélie penguins breeding at King George Island, Antarctica determined by dead reckoning techniques from bird-attached loggers. I consider the fine scale patterns of movement of birds and the extent to which particular movement types result in specific rates of displacement. Consideration is given to the function of particular movement types.

Materials and methods

Field work was conducted at Ardley Island ($62^{\circ}13'S$, $58^{\circ}55'W$), Antarctica during December 1991 and January 1992 and consisted of equipping 18 Adélie penguins brooding chicks with data loggers to record aspects of their foraging behaviour. Units were attached, using tape as described in Wilson *et al.* (1997), to the dorsal midline of the birds' backs, taking care to place them posteriorly so as to minimize drag (Bannasch *et al.*, 1994). The devices were left in place for a minimum of one foraging trip before being recovered and the data were accessed by connection of the units to a computer with an RS 232 interface.

The loggers, which were streamlined and measured $150 \times 57 \times 37$ mm (mass 200 g), had 6 channels to record information in a memory of 64 kbyte (see Wilson *et al.*, 1993 for details). These channels recorded depth (1 channel, 10 bit resolution) via a pressure transducer, swim speed (1 channel, 8 bit resolution) by counting the number of rotations of a paddle wheel, bird heading (2 channels, 8 bit resolution) using Hall sensors to determine the position of a magnetic compass needle, light (1 channel) and temperature (1 channel). The two latter channels are not relevant to this work and will not be further discussed here. The pressure transducers were calibrated in a pressure tank before and after the field season and found to be good to within 0.5 m. The speed sensors were calibrated by equipping Adélie penguins with the units, set to record speed once every second, and then letting the birds swim up and down a 21 m swim channel (for details see Culik and Wilson (1991)) at will while recording the position (and thus the speed) of the birds at all times. Swim speed could be resolved to within 0.1 m/s for speeds in excess of 0.4 m/s. Independent tests of the compass showed that the heading could be resolved to within 12° for dive angles up to 17° . During deployments of the units on free-living birds data were recorded at intervals of once every 10 or 15 s.

The data acquired from the loggers were analysed using two programmes from Jensen Software Systems (Laboe, Germany). The diving behaviour was assessed using ANDIVE which determines the start and end times of all dives in addition to the times of points of inflection within the dive, these being nominally the start and end of the bottom phase. The programme thus provided data on the dive durations, descent, bottom and

ascent durations, as well as descent, bottom and ascent rates and (after integrating the effects of measured swim speed) angles. A random sample of the dives was then selected for statistical treatment (STATEASY, Lozan, Hamburg, Germany). In addition, the data on speed, heading and depth were also treated with a vectorial analysis (using ROUTE version 10.0) so as to determine the 3 dimensional routes of the birds during foraging (Wilson, 2001). Routes thus calculated are not perfect since they are liable to drift errors which occur when birds move to areas with appreciable water currents. The extent of the drift can be determined, however, if the known start and end positions of the route are compared to those calculated by the programme. Drift errors were minimized by forcing the calculated start and end positions to accord with the known start and end positions and correcting all points along the route minimally to accord. Output files were produced from this programme giving bird position at each measurement as x , y and z co-ordinates (x corresponding to the number of metres to the North or South of the start position, y to the number of metres East or West and z to the depth). Subsequently, only the x and y co-ordinates were considered and the horizontal displacement of birds calculated using

$$D = \sqrt{[(x_n - x_{n+1})^2 + (y_n - y_{n+1})^2]},$$

where D is the horizontal displacement and (x_n, y_n) and (x_{n+1}, y_{n+1}) define the position of the birds at time $t=n$ and $t=n+1$.

In order to quantify the qualities of the foraging track, an index of deviation from a straight line course was applied. This index was the total distance travelled by a bird over a particular time interval divided by the straight line distance travelled over that time. Mathematically, the travel index (TI) was:

$$TI = \frac{\sum_{n=0}^{n=p} \sqrt{[(x_n - x_{n+1})^2 + (y_n - y_{n+1})^2]}}{\sqrt{[(x_n - x_p)^2 + (y_n - y_p)^2]}}$$

over a time interval denoted by p readings. Thus, high values denoted extensive non-directional movement while a value of 1.0 indicates that the animal travelled in a perfectly straight line.

Results

All birds were recovered in good condition after they had been foraging for at least one trip and all appeared to have foraged successfully as evidenced by the state of the chicks. However, this was ascertained in 7 cases with certainty since the birds were actually observed feeding chicks. I did not monitor mass changes in the equipped birds because my experience is that the process of weighing them in a bag is particularly stressful. After the devices were removed birds apparently continued breeding normally in a manner identical to that of unequipped conspecifics.

Foraging trip length was highly variable, ranging from 32 to 1243 min (mean=232 min, SD 282, N=18) but appeared to be essentially bi-modal, with 8 trips (44%) being less than 100 min and 9 (50%) being between 160 and 300 min. A final trip was well in excess of this at 1243 min. Observations from the island indicated that the very short

foraging trips consisted primarily of birds that left the island to join local feeding groups of penguins that were visible from the shore.

Maximum depth reached by any bird during the trips was 97 m although over 90% of all dives were executed to depths less than 70 m. Dives could be readily differentiated into a descent, bottom and ascent phase. The duration of all of these parameters increased as a function of maximum depth reached (Table 1). However, the rates of change of depth during the descent and ascent phases also increased with increasing maximum depth reached so that time spent per metre depth in the water column was less in birds diving deeply (Table 1). Overall, the total time spent as a function of depth

Table 1. Summary of dive parameters (y) as a function of depth (x) for three Pygoscelids.

Species	Variables	Descent duration	Bottom duration	Ascent duration	Surface interval
Adélie	Best fit	$y = a + (bx)$	$y = a + (b/x)$	$y = a + b (x^{0.5})$	$y = a + b (x^{0.5})$
	R^2	0.54	0.26	0.42	0.29
	a -value	14.20	30.79	9.13	4.47
	b -value	0.389	-76.23	4.01	4.83
	P	<0.001	<0.001	<0.001	<0.001
Chinstrap	Best fit	$y = a + (bx)^2$	$y = a + b \ln (x)$	$y = a + (bx)$	$y = a + b (x^2)$
	R^2	0.53	0.48	0.50	0.20
	a -value	3.50	-6.21	12.66	19.80
	b -value	0.04	10.46	0.45	0.009
	P	<0.001	<0.001	<0.001	<0.001
Gentoo	Best fit	$y = a + (bx)$	$y = a + b \ln (x)$	$y = a + (bx)$	$y = a + b (x^2)$
	R^2	0.40	0.17	0.22	0.10
	a -value	17.31	-7.57	20.77	20.97
	b -value	0.46	10.37	0.35	0.005
	P	<0.001	<0.001	<0.001	<0.001

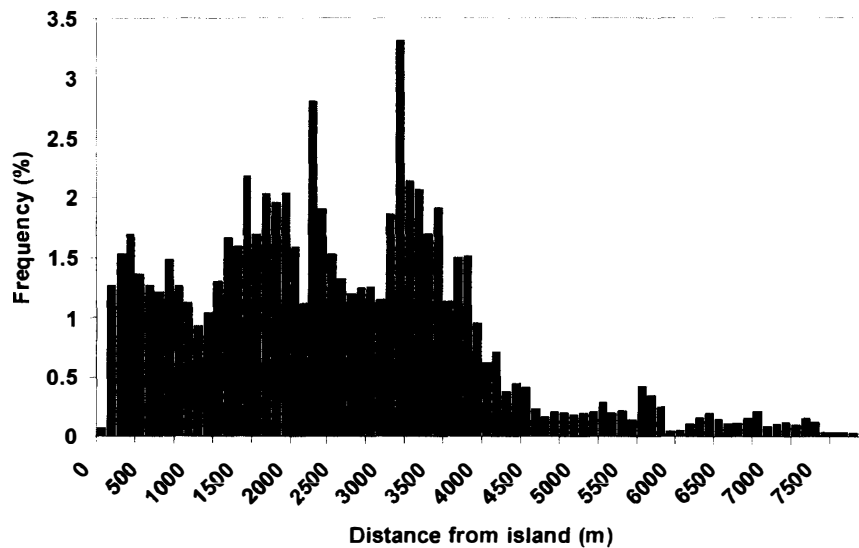


Fig. 1. Frequency of time spent as a function of distance to the breeding colony for Adélie penguins foraging for chicks around Ardley Island during the 1991/2 austral summer.

could be determined by consideration of the above parameters and the frequency of maximum depths reached. The final time at depth usage of Adélie penguins from Ardley Island was thus less time with increasing depth although there was plateau between about 20 and 70 m.

The farthest distance from the breeding site (straight line distance to the farthest point) reached by any one bird was 35 km during a 21 h foraging trip. However, the time spent as a function of distance from the colony for all birds demonstrated that 71.3% of all time at sea was spent within 10 km of the island (Fig. 1). This time/distance relationship was primarily affected by the form of the foraging routes since there was considerable variability in the directionality of the tracks over the course of the foraging trip (Fig. 2). Highly directional travelling displaced birds rapidly and thus reduced the time they spent in any one zone, whereas non-directional movement resulted in extensive accumulated time in limited regions. In this regard, subjectively (but see below), the foraging tracks appeared to be composed of 3 major types of movement; (i) periods of highly directional travelling where birds essentially travelled in a straight line, (ii) periods where bird movement appeared to describe interlinking arcs of varying radii (typically between 10 and 100 m) but where heading differences between fixes were almost invariably less than 90° and (iii) periods where birds moved within a very limited area consisting of some tens of square metres and where heading differences between fixes varied between 0 and 180° (Fig. 2). According to the travelling behaviour of the birds, the travel index, a non-subjective description of the degree of deviation in the swim course (see methods), showed considerable variability, ranging from 1.0 (birds travelling in a perfectly straight line) to over 50.

Travel index (TI) varied during the course of the foraging trip (Fig. 3) generally exhibiting highly directional travelling at the beginning and end of foraging trips as birds displaced themselves between colony and foraging site. However, low TIs were also apparent during virtually all phases of the foraging trip, where birds moved rapidly from one foraging area to another (Fig. 3). Changes in the scales over which birds moved directionally or otherwise could be alluded to by examining changes in TI over different time periods. For this work I considered periods from 100 to 1000 s because 100 s represented 10 consecutive readings and 1000 s is less than 10% of the mean total foraging trip length (see earlier) so that the form of the looping course necessary in birds returning to the colony should not be obvious in the TI . Most variability in TIs over time was shown in indices calculated for short time periods (Fig. 3) with TI changing from just over 1 to values in excess of 10 within 100 s. However, if the temporal variability in TI is ignored and the frequency of various TI values calculated for the whole foraging trip, it can be seen that the TIs calculated for the longer time intervals had the greatest spread (Fig. 4) although there was appreciable inter-bird variability (Fig. 5). Generally, over all time intervals, the larger the TI , the less often it occurred. This means that Adélie penguins spent most of their time at sea swimming in a virtually straight line with a decreasing tendency to decrease from this straight line path with increasing deviation. Of a large number of different curve fits attempted, the lines of best fit of percentage time (mean for all birds) spent engaged in particular travel indices (TI ; for $TIs > 1.1$) followed the general form of:

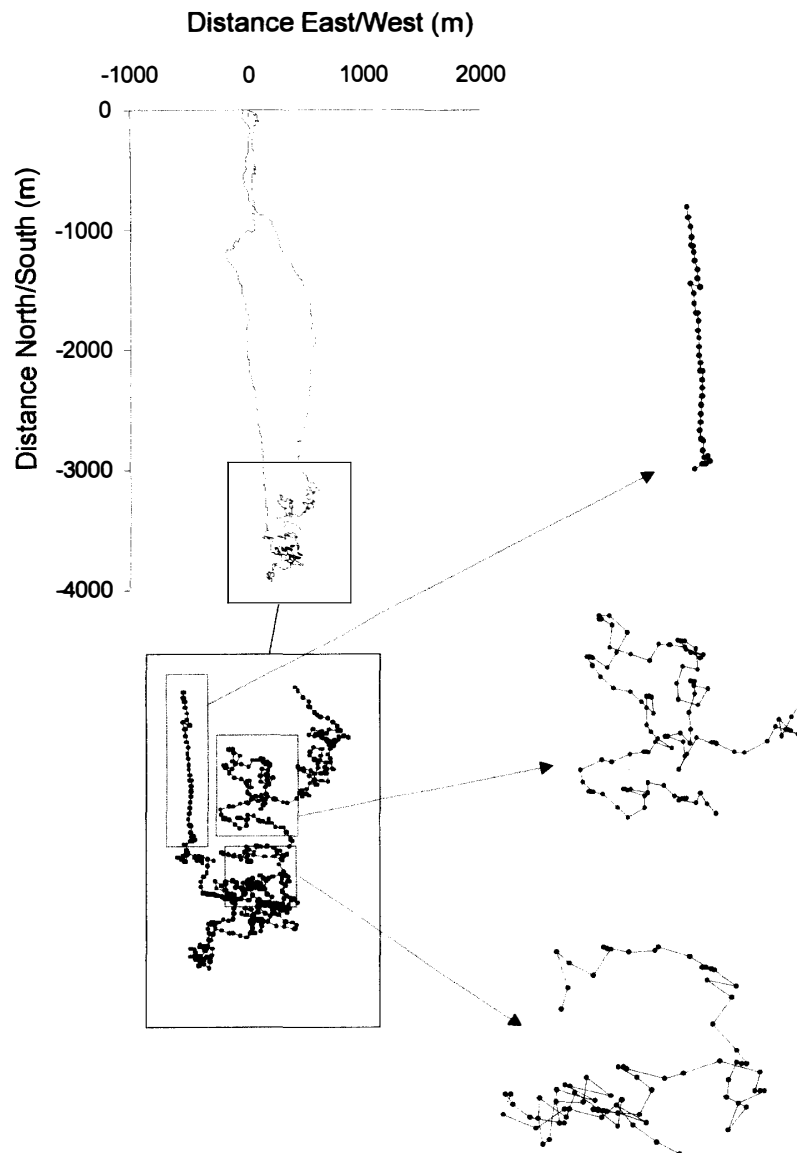


Fig. 2. Example of a foraging track of an Adélie penguin foraging for chicks around Ardley Island during the 1991/2 austral summer. The expanded regions show the various types of travelling behaviour; upper right—highly directional travelling, centre right—circling behaviour, lower right—circling behaviour followed (bottom of trace) by highly localised movement. Data recorded at 10 s intervals are indicated by dots.

$$\text{Frequency (\%)} = (a + b/(TI)^2)^2,$$

where a and b are constants (Fig. 5). This was the case irrespective of the interval over which the travel index was calculated, with correlation coefficients ranging from $r^2=0.90$ to 0.99.

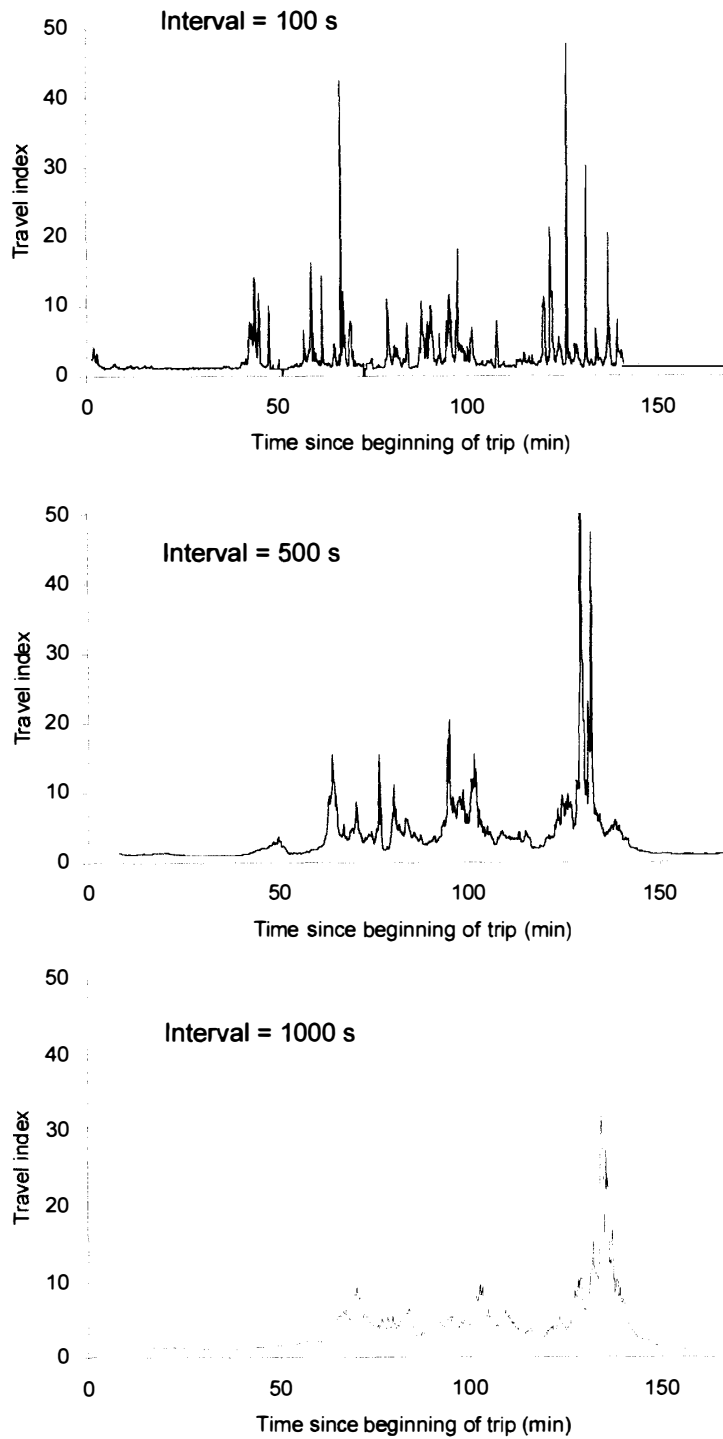


Fig. 3. Travel indices (total distance travelled by a bird over a particular time interval divided by the straight line distance travelled over that time) for three different time intervals for the penguin whose foraging trip is shown in Fig. 2.

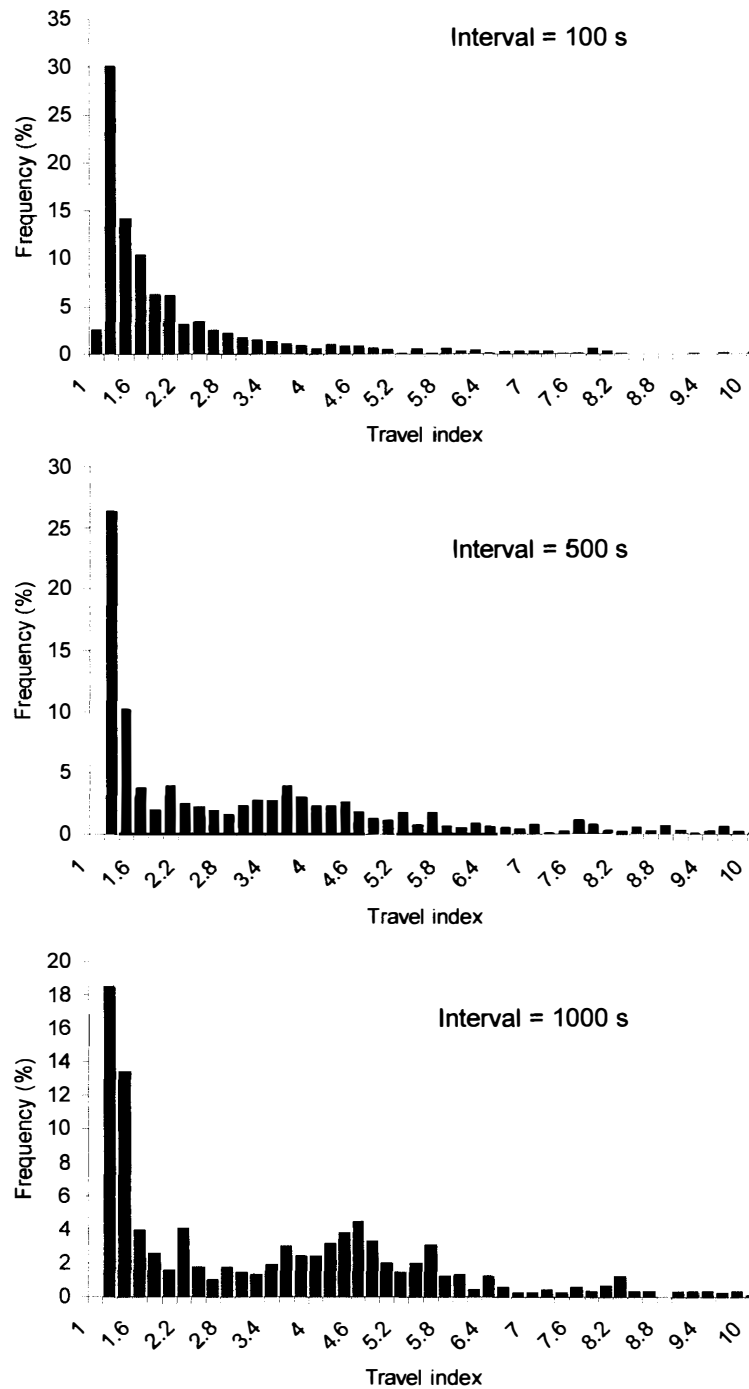


Fig. 4. Frequency distribution of travel indices for the penguin whose foraging trip is shown in Fig. 2 (*cf.* Fig. 3) for values taken over different time intervals.

Discussion

Vertical movement

There has been considerable work conducted on the diving behaviour of free-living Adélie penguins using time-depth recorders (*e.g.* Naito *et al.*, 1990; Wilson *et al.*, 1989a,

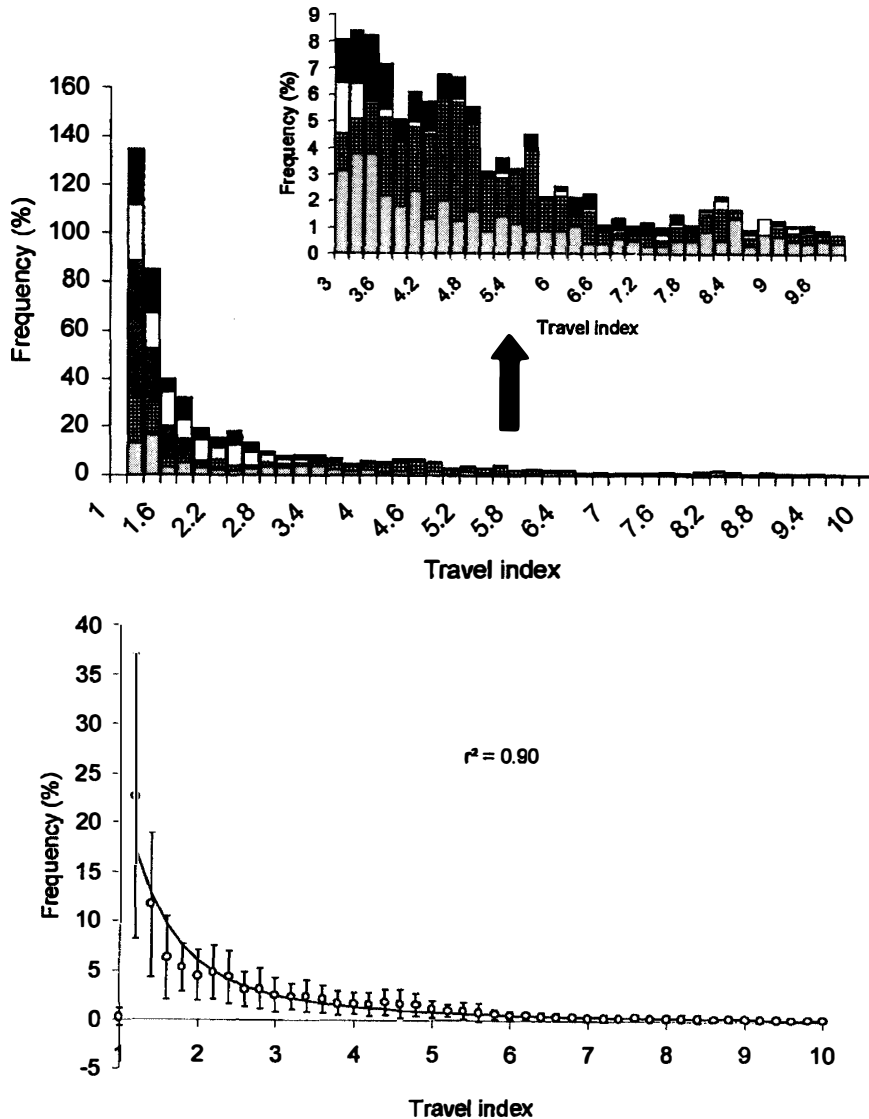


Fig. 5. Upper: Frequency of various travel indices (taken over 100 s intervals) for five different foraging trips of Adélie Penguins from Ardley Island (five were chosen because inclusion of more in the diagram did not allow individual trips to be easily discerned). Each different shaded block refers to data from a different bird, the maximum values representing the sum for all birds. Note that, for scaling reasons and ease of viewing, data for values between 1 and 1.5 have been omitted. Note also that these data do not include the bird shown in Fig. 4. Lower: Mean frequency (and SD) of various travel indices for all Adélie penguin foraging trips for indices calculated over a measurement interval of 100 s together with the corresponding best curve fit.

1991; Chappell *et al.*, 1993; Watanuki *et al.*, 1993, 1997; Rodary *et al.*, 2000, Ropert-Coudert *et al.*, 2001) which demonstrates that this species is capable of exploiting depths of up to 180 m (Whitehead, 1989) but tends to concentrate most foraging activity in the upper 80 m of the water column. The form and function of the dive profiles as well as the time at depth have been extensively discussed by Wilson *et al.* (1993) and Ropert-Coudert *et al.* (2001). Dive depths appear to be primarily determined by the distribution

of the prey (Wilson *et al.*, 1993; Watanuki *et al.*, 1993; Ropert-Coudert *et al.*, 2001) *Euphausia superba* (e.g. Ainley *et al.*, 1998 and refs therein), but also on the constraints of the environment (Watanuki *et al.*, 1993, 1997). The data recorded from this study on the diving behaviour of Adélie penguins accord closely with data gathered in other studies and, as such, will not be further discussed here.

Horizontal movement

There is little information on the movement of Adélie penguins during the chick-rearing period although, based on trip duration and some radio telemetric data (Trivelpiece *et al.*, 1986), Trivelpiece *et al.* (1987) speculated that foraging ranges probably do not much exceed 43 km (Trivelpiece *et al.*, 1987). Davis *et al.* (1988) and Sadleir and Lay (1990) fitted VHF transmitters to Adélie penguins during the chick-rearing period and found that birds generally foraged within 15 km of the colony although a later study by Kerry *et al.* (1995) using satellite telemetry documents birds that may range further than 100 km (*cf.* Clarke *et al.*, 1999; Wienecke *et al.*, 2000). The limited foraging range concurs with our data. However, satellite and VHF telemetry data do not give detailed information on the movement over short time scales so that the patterns of movement observed in our study are not apparent in telemetric studies.

The function of the movement observed in our study can be alluded to by consideration of the travel indices. Virtually straight line travel (*TI* values of around 1) results in such rapid movement of birds that the function of such behaviour can only be displacement of birds between breeding and foraging sites or movement between sites deemed advantageous for foraging. The exponential decay of the frequency of occurrence of travel indices with increasing values over all time scales considered indicates that Adélie penguins consecrate *ca.* 35% of all their time at sea to displacement of this type (e.g. Fig. 5).

Conversely, high *TI* values (>5) show that birds are capable of being extremely active within a highly confined area. This movement is almost certainly due to prey capture since the principal prey of these birds is Antarctic krill (see Williams, 1995 for review) which occur in patches (Nicol and de la Mare, 1993). There is little information on the horizontal displacement of Adélie penguins feeding on krill (but see Zusi, 1975) although recent logger studies demonstrate that feeding birds return repeatedly to exploit the same depth (Ropert-Coudert *et al.*, 2001) and thus presumably displace themselves little. Given that high *TI* values are likely to be indicative of prey exploitation, future studies could examine the location of such high values to allude to the distribution of krill.

TI values of between *ca.* 1.3 and 5 are more problematic to interpret. Although fine-scale data on the movement of marine animals in the wild are extremely scarce, there has been considerable interest in the concept that animals might exhibit a Lévy motion (a special class of random walk whose step lengths are not constant but rather chosen from a probability distribution with a power-law tail) (Larralde *et al.*, 1992; Viswanathan *et al.*, 1996, 1999). However, the detection of any discernable systematic search pattern in animal movements would eliminate this possibility, at least over the scale being considered. That Adélie penguins display circles in their search strategy indicates that, at least over a scales of tens of metres, Lévy movement is not applicable. Under what sort of conditions, then, might circles be produced in the movements of a searching animal? The circles exhibited by Adélie penguins are highly variable, with diameters ranging from

ca. 200 to about 20 m (and likely less because the sampling frequency of the compass did not allow finer resolution) (see Fig. 2). A precise determination of the frequency distribution of the dimensions of circles using the travel index is not possible because the maximum TI obtainable based on a semi-circle is $\pi/2$ or about 1.6 and our values are often considerably higher than this indicating that circles occur within circles tending to increase TI values. Manual determination of the frequency distribution of circle diameter would require considerable effort but, in the interests of comprehension, should perhaps be undertaken. Whatever the case, circular movement implies that the birds are receiving sensory information that can be used by them to hone in on prey concentrations (*cf.* Montgomery *et al.*, 1999) although the possibility that birds may be simply moving to areas known to contain higher prey concentrations cannot be excluded. I consider that vision is unlikely to be used in this regard because the visibility underwater in the King George area does not allow animals to see over many tens of metres and, in any event, after visual location of a prey aggregation (or a cue to it, such as aggregations of other birds feeding), one would expect the penguin to swim directly to the prey. This would not produce a circular pattern. I suggest, rather, that Adélie penguins may be using olfactory (or gustatory) cues to locate prey at this scale. Refined olfactory capabilities have been demonstrated in procellariiforms (Nevitt *et al.*, 1995; *cf.* Turner *et al.*, 1995) and certainly the ability to locate prey aggregations using such a system would be highly advantageous for penguins (*cf.* Nevitt, 2000; Vickers, 2000). In this regard, the circular movements shown by Adélie penguins could be explained by a predator determining the location of prey according to differences in concentrations of particulate matter which can only be sampled by the animal moving along and across gradients. Further research is needed in this field to elucidate the matter.

Although the birds in this study showed similar percentages of time consecrated to particular types of movement (*cf.* Fig. 5), this is not to be expected across years and between different foraging sites (*e.g.* Watanuki *et al.*, 1997; Yoda *et al.*, 2001) and comparison of the goodness of fit from data derived from birds in different regions fitted with the compass system may prove a useful tool to assess prey abundance and proximity to the colony. Where the goodness of fit decreases it should be possible to examine which elements of the movements in the foraging trip have changed to result in this. Increased highly directional travelling would indicate, for example, that prey are more spaced. In this respect it is notable that Boyd (1996) found two modes of fur seal movement and suggested that the occurrence of one type or another is related to krill swarm structure. Despite proposed variability, it is interesting that Adélie penguins appear to have apparent fixed action patterns in some aspects of their foraging behaviour. Whether such behaviour stems from genuine fixed action patterns or is a response to environmental conditions that tends to lead to a particular type of movement dictated by stable conditions in the Ardley Island area remains to be seen.

The complexity of 3 dimensional movement of marine predators such as penguins means that it is likely to take considerable time before movement patterns can be properly elucidated and the value of particular behaviours assessed. In this regard, the use of dead reckoning systems, such as that presented here, can be enormously enhanced by being coupled with other measures of activity such as systems for determining food ingestion (Wilson *et al.*, 1992; Ancel *et al.*, 1997; Ropert-Coudert *et al.*, 2000, 2001) or activity

via acceleration (Yoda *et al.*, 1999, 2001). The coupling of systems will undoubtedly happen and our understanding of the role of the penguin within the ecosystem will benefit enormously as a result.

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