

## Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator

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In large marine predators, foraging entails movement. Quantitative models reveal how behaviours can mediate individual movement, such that deviations from a random pattern may reveal specific search tactics or behaviour. Using locations for 52 grey seals fitted with satellite-linked recorders on Sable Island; we modeled movement as a correlated random walk (CRW) for individual animals, at two temporal scales. Mean move length, turning angle, and net squared displacement ( $R_n^2$ : the rate of change in area over time) at successive moves over 3 to 10 months were calculated. The distribution of move lengths of individual animals was compared to a Lévy distribution to determine if grey seals use a Lévy flight search tactic. Grey seals exhibited three types of movement as determined by CRW model fit: directed movers – animals displaying directed long distance travel that were significantly underpredicted by the CRW (23% of animals); residents – animals remaining in the area surrounding Sable Island that were overpredicted by the model (29% of animals); and correlated random walkers – those (48% of animals) in which movement was predicted by the CRW model. Kernel home range size differed significantly among all three movement types, as did travel speed, mean move length, mean  $R_n^2$  and total distance traveled. Sex and season of deployment were significant predictors of movement type, with directed movers more likely to be male and residents more likely to be female. Only 30% of grey seals fit a Lévy distribution, which suggests that food patches used by the majority of seals are not randomly distributed. Intraspecific variation in movement behaviour is an important characteristic in grey seal foraging ecology, underscoring the need to account for such variability in developing models of habitat use and predation.

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Most animals must move to locate and capture food. Thus, patterns of movement are considered a key factor in the survival of most organisms (Turchin 1998, Bergman et al. 2000). In any given environment, there is a range of behaviours (i.e. phenotypes) that can be considered successful. These can be learned behaviours, or alternatively, the products of longer-term selection for specific traits (Komers 1997). Intraspecific variation in movement behaviour reflects the different tactics used by individuals or sexes within a species or population to

meet the demands of survival. We expect natural selection to favour those strategies that maximize fitness or some proxy of fitness, such as the rate of resource acquisition, or production of offspring. Given that natural selection operates at the level of the individual, ecological models that lump all individuals into the same behavioural category effectively disregard this variation (Judson 1994, Zollner and Lima 1999). Consequently, examining average responses across populations obscures variability in behavioural ecology. Animal move-

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ment often becomes most intriguing by examining how individuals fail to fit model predictions (Bergman et al. 2000).

One difficulty in studying movement patterns within a population lies in distinguishing one pattern from another. Ecologists interested in movement patterns have used mathematical models to bring studies of movement out of the purely descriptive realm (Kareiva and Shigesada 1983, Root and Kareiva 1984, Viswanathan et al. 1996, Barrett and Lowen 1998). Perhaps the simplest means of quantitative description is that of home range (Burt 1943). Kernel methods of estimating home range produce a density estimate that can be interpreted as a utilization distribution (Worton 1989) and are useful because they provide an indication of the key areas used by an individual (Worton 1995). Home range analysis has a long history in terrestrial wildlife ecology (e.g. Damuth 1981, Bowen 1982, Anderson and Rongstad 1989). However, the difficulty with home range indices is that they provide a single picture of the area occupied by an animal's trajectory, without lending any understanding to the decision rules which led the animal to move across the landscape in such a manner.

In contrast, a Lagrangian approach to modeling focuses on aspects of the moving individual; for example, velocity or direction can be used to derive information about an animal's trajectory and delineate the search strategies employed (Turchin 1998). Instead of a single picture, individual modeling projects movement patterns along a continuum, such that decisions over time and their influence on the resulting distribution can be described in terms of the behavioural mechanisms involved (Zollner and Lima 1999).

The simplest stochastic model is that of Brownian motion; this is the basis of the classical "random walk". However, this model does not consider the cephalo-caudal polarization which gives the tendency for an animal to go forward, and thus does not give an accurate representation of most animal movement (Bovet and Benhamou 1988). Alternatively, a correlated random walk (CRW) assumes independent distributions of move lengths and turning angles that describe an animal's movement trajectory. Although each step length or turning angle is randomly chosen, a probability distribution can be derived which allows the formulation of equations that predict the probability of future behaviour (Shlesinger 2001). By examining departures from a random walk, we may gain insight into the foraging behaviour of individuals and the variability in search tactics used while foraging.

More recently, ecologists have borrowed concepts from the physical sciences to determine optimal search strategies for randomly located objects (Viswanathan et al. 1996, 1999, Atkinson et al. 2002, Mårell et al. 2002). Rather than considering a normal Gaussian or Rayleigh

distribution of trajectory lengths of a randomly foraging animal, Viswanathan et al. (1999) suggest that an inverse square power-law distribution of move lengths, a Lévy distribution, is a more optimal strategy because it results in a greater number of patches being visited, with fewer repeat visits. Such distributions are characterized by many short moves and few large displacements. Evidence of Lévy flights have been found in foraging ants (Shlesinger 1986), *Drosophila* (Cole 1995), wandering albatross, *Diomedea exulans* (Viswanathan et al. 1996), reindeer, *Rangifer tarandus tarandus* (Mårell et al. 2002), and jackals, *Canis adustus* (Atkinson et al. 2002).

To date, our knowledge of the movement patterns of large predators have been limited by the sheer spatial scale of their ranges. Consequently, the rules that influence movement patterns and distributions of larger animals in relation to food resources remain poorly understood. In contrast, the movement of insects and smaller animals has received more attention, resulting in the modeling of individual movements, population distribution and scale-specific resource use (Kareiva and Shigesada 1983, Cain 1985, Bovet and Benhamou 1988, Turchin 1991, Gustafson and Gardner 1996).

Understanding the foraging behaviour of marine predators has presented an even greater challenge, given that nearly all foraging takes place beneath the surface of the water. With recent advances in satellite telemetry, we have begun to produce qualitative descriptions of the movement of large marine predators, including pinnipeds, (Stewart and DeLong 1995, Folkow et al. 1996, McConnell and Fedak 1996), cetaceans (Read and Westgate 1997, Mate et al. 1998, 2000), seabirds (Davis et al. 1996, Hull et al. 1997), polar bears (Ferguson et al. 1997), and turtles (Polovina et al. 2000). Nevertheless, few studies have modeled the movement patterns used by large predators in a quantitative manner. Given that individual movement behaviour drives population spatial structure and resource use (Turchin 1998), this is a substantial gap in our understanding of these animals (Bergman et al. 2000).

In this paper we apply quantitative models of movement to satellite derived trajectories of a large marine predator, the grey seal, *Halichoerus grypus*. Grey seals are abundant apex predators inhabiting both sides of the North Atlantic and there is increasing evidence that marine mammals can have significant top-down effects on ecosystem functioning (Estes 1996, Bowen 1997). In recent years, there have been several attempts to model the impact of pinniped predation on commercially important fish stocks (Overholtz et al. 1991, Punt and Butterworth 1995, Mohn and Bowen 1996). A significant limitation of these models is our lack of understanding of how foraging is distributed in time and space.

We had two main objectives in this study. Firstly, we tested the applicability of CRW and Lévy flight models

to predict the trajectories of individual grey seals at two temporal scales of movement. We tested the null hypothesis that all grey seals moved in the same random fashion. Secondly, we examined sex, age, season, and body mass as predictor variables of the type of movement exhibited by grey seals, and considered the individual variability in movement patterns with movement type. Since sex effects have been found in grey seal diving behaviour (Beck et al. 2003a, b), we predicted that sex might also be an important factor in structuring movement patterns in grey seals. Given the variability in prey characteristics in marine ecosystems, we expected that foraging experience and seasonal changes in prey availability might affect search tactics thus giving rise to age and season effects. We regard these analyses as the first steps toward a better understanding of the spatial distribution of foraging in marine apex predators.

## Methods

### Study area

The study was conducted on Sable Island (44°53'N, 60°00'W) a vegetated sand bar approximately 300 km from Halifax, Nova Scotia, Canada from June 1995 to January 2002 (Fig. 1). Sable Island is the largest breeding site for grey seals worldwide. The number of pups born on Sable Island has been increasing exponentially for four decades and in 1997 more than 25000 pups were born (Bowen et al. 2003).

Known-aged, adult grey seals were captured using hand-held nets (Bowen et al. 1992) and weighed to the nearest 0.5 kg prior to being anaesthetized with Telazol (equal parts of Tiletamine and Zolazepam). Males and females received an average dose of 0.45 mg kg<sup>-1</sup> body mass and 0.90 mg kg<sup>-1</sup> body mass, respectively (Bowen

et al. 1999). Once the animals were anaesthetized, dorsal standard length (McLaren 1993) was measured.

To study the pattern of movement, animals were instrumented with satellite-relay data loggers (SRDL – Wildlife Computers, Redmond WA or ST-18 – Telonics, Mesa AZ). Instruments were secured to netting and then the netting was attached to the pelage on top of the head or neck of the anaesthetized animals using 5-min epoxy. A salinity sensor on the instrument detected whether the animal was wet or dry and suppressed transmissions when the instrument was wet. Most instrumented seals returned to Sable Island during the breeding season in December/January, at which point they were re-weighed and the satellite transmitter was removed.

Instrumented females were not recaptured until several days postpartum to permit females to form a strong bond with their pup. The rate of mass lost by females during the first 5 d of lactation is linear at 4.3 kg d<sup>-1</sup> (Mellish et al. 1999). Thus, we corrected the mass at recapture to initial postpartum mass to estimate the total mass gained during foraging. Similarly, male grey seals were usually captured within several days of appearing on the island in December/January. We used the average daily mass lost during the breeding season (2.5 kg d<sup>-1</sup>, Godsell 1991), to back-calculate male body mass on arrival.

### Data processing

Satellite transmitters were duty cycled to transmit for 8 h every day or every 2nd day to conserve battery power and reduce satellite fees. Locations of grey seals were determined from data collected by polar orbiting satellites operated by Service Argos. The latter provides a location quality index (LQ) for each estimated location. Standard locations (LQ = 3, 2, 1 and 0) have known theoretical precision, but auxiliary locations (LQ = A or B) do not (Priede and French 1991). Calibration studies have shown that considerable location errors can occur for all location qualities (Hull et al. 1997, Le Boeuf et al. 2000). Therefore, all locations for each seal (including auxiliary locations) were filtered using a three-stage algorithm (Austin et al. 2003) to remove erroneous data. We used these filtered data in subsequent analyses.

To estimate the overall area used by individuals, kernel home ranges (Worton 1989) were calculated using the Animal Movement Extension (Hooge and Eichenlaub 1999; available on <http://www.absc.usgs.gov/glba/gis-tools.htm>) in Arcview 3.1 (Environmental Systems Research Institute, Inc. 1996). Fixed-kernel home ranges at the 50% and 95% utilization distributions were calculated based on mean daily locations, and mean bi-daily locations using least squares cross-validation (LSCV) to select the smoothing factor. Seaman and

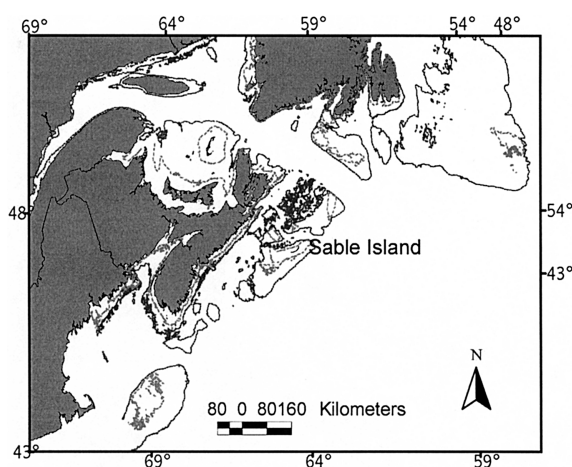


Fig. 1. Map of study area showing Sable Island. Dark grey lines represent the 100 m isobath, and light grey lines represent the 50 m isobath.

Powell (1996) demonstrated that the fixed-kernel estimator using LSCV provided the least biased and most accurate measure of home range size, particularly on data that is multi-modal and non-normal.

We used the Kareiva and Shigesada (1983) modification of the CRW model of Skellam (1973) to calculate the net squared displacement ( $R_n^2$ ) of individuals. This model measures the rate of change in area over time by incorporating move lengths (the measured distance from one location to the next) and turning angles (the change in angle from one location to the next) into a quantitative description of an animal's trajectory (Turchin 1998). We calculated the net squared displacement  $R_n^2$  for each seal at successive moves, assuming that there is no predisposition to turn in a preferential direction (Turchin 1998):

$$R_n^2 = nl^2 + 2l^2 \frac{c}{1-c} \left( n - \frac{1-c^n}{1-c} \right)$$

where  $R_n^2$  (km) is the displacement from the first location,  $n$  is the number of moves from the first location,  $l$  is mean move length (km) and  $c$  is the mean of the cosines of the turning angles.

Using the empirical distribution of move lengths and turning angles from all grey seals, an expected  $R_n^2$  was generated using a bootstrapped simulation of 10000 iterations, with 95% confidence intervals determined by the percentile method (Turchin 1998). The observed (O) and expected (E)  $R_n^2$  were plotted over time to visualize how each seal fit the correlated random walk model – the null hypothesis. In most cases it was clear if the seal fit the model or not, but in some cases the track crossed the 95% confidence interval for some portion of the track. To determine if seals fit the model, we developed a statistical  $I_p$  which provided an index of the proportion of the track that was outside of the confidence limits:

$$I_p = \sum_{i=1}^n \left[ \frac{(E_{ui} - O_i) \times j}{E_{ui} - E_{mi}} + \frac{(E_{li} - O_i) \times k}{E_{li} - E_{mi}} \right]$$

where (i) = 1...n locations,  $j = 1$  if  $O > E_u$  and  $j = 0$  if  $O < E_u$ ,  $k = 1$  if  $O > E_l$  and  $k = 0$  if  $O < E_l$ , and  $u$  and  $l$  are the upper and lower 95% confidence limits.

The 95th percentile of the expected values was used as the critical value and compared to the observed trajectories. All seals with an observed  $I_p$  greater than the critical value were considered to significantly differ from the CRW model. Those animals that fit the model were termed correlated random walkers (CRWs). An individual's trajectory was overpredicted by the model if the observed track lay below the expected  $R_n^2$ ; hereafter, these individuals are termed residents because they had a lower displacement than predicted by the model. If the observed trajectory was above the expected  $R_n^2$ , these individuals had a greater displacement than predicted by the model and were termed directed movers.

Due to the nature of seal diving behaviour and satellite coverage, there are occasional days in which no locations were available for some animals. To determine if missing days in the satellite record would affect the fit to the CRW model, we randomly removed from 1 to 12 consecutive daily locations from the 30 seals with complete records and generated 1000 simulated tracks of each individual and level of deletion. At each level of deletion, the animals were classified as fitting the CRW model or not, and these results were compared with the original data.

Our simulations showed that data quality could affect the overall results of CRW fit. As expected, increasing the size of the missing data gap increased the overall distance traveled per move length- thus, animals appeared to have greater overall move lengths. Prior to deleting daily locations from those seals, 25 animals fit the CRW model, 15 animals were overpredicted by the model, and 12 animals were underpredicted. Of the observed animals having missing data, the mean duration of the gap was  $4.2 \pm 0.72$  days. Using simulations with 4 missing locations, 31 animals fit the CRW model, 10 animals were overpredicted by the model, and 11 animals were underpredicted. Thus, when data was missing, we were more likely to overestimate the number of animals that fit the CRW. Nevertheless, the objective of this paper was not to examine the proportion of movement types, but instead to examine inherent variability in movement types, which seems not to have been affected by a modest amount of missing data.

To assess whether significant directionality occurred in the distribution of turning angles between successive moves, mean turning angles were calculated for each individual seal (ranging from  $-180^\circ$  to  $180^\circ$ ), and across each movement type using circular statistics (Batschelet 1981). Rayleigh's test statistic was used to test the null hypothesis that the distribution of turning angles was random (Batschelet 1981). Angular concentration, whether the angles were uniformly distributed around a  $360^\circ$  circle, was measured by calculating a mean vector ( $r$ ) for each animal (Batschelet 1981).

To test for the presence of autocorrelation between successive turn angles, we used a non-parametric approach to estimate the autocorrelation function (ACF). We estimated the mean autocorrelation coefficient between pairs of turn directions at lags up to six moves (Turchin 1998). An ACF was considered significant if greater than 2 standard errors from zero. Autocorrelations between successive move lengths were tested using Pearson's correlation coefficient (Nolet and Mooij 2002). Other location statistics such as mean distance traveled, total distance traveled, and overall linearity of trajectories were measured using the Animal Movement Extension in Arcview. An index of linearity (LI) of each trajectory was calculated as the distance

between the first and last point divided by the total distance traveled.

The distribution of move lengths was also examined to see if it fit a Lévy distribution:  $P(l) \sim l^{-\mu}$ , where  $l$  is move length and  $\mu$  is a fitted parameter taking on values of  $1 < \mu \leq 3$  under a Lévy flight (Viswanathan et al. 1999, Mårell et al. 2002). For each seal, move lengths between successive locations were divided into fifteen equal bins, and the frequency of move lengths in each bin calculated. We estimated the Lévy parameter  $\mu$  from a regression of log frequency on log move length, and then examined trends in residuals that would indicate lack of fit.

To investigate how each seal moved relative to the common initial location, distance from Sable Island was calculated at successive satellite locations. Trip duration was calculated as the period from the time a seal left a "box" extending 20 km in all directions from the island until the seal once again entered this box. We adopted this approach because location errors associated with Argos data meant that locations within this box could not be reliably determined as being on or off the island. Given that most of our grey seal locations were of LQ = 0 and LQ = A, we chose the distance of 20 km because it is roughly the midpoint of the mean error of these Argos satellite location classes (9.3 km and 28.3 km, respectively, Le Boeuf et al. 2000).

To compare movement characteristics of those seals that fit the CRW model and those that did not fit the model, we used a single factor MANOVA on six movement variables (kernel home range size at the 95% utilization distribution, mean move length, total distance traveled, index of linearity, mean vector, mean speed and mean net squared displacement). Although it is possible that oceanographic influences might affect movement patterns of marine organisms on an inter-annual basis (Boyd et al. 1994, Thompson et al. 1996), for the purpose of this study, year of deployment was treated as random variation. Sample size was not large enough to look at season and year simultaneously. Where multiple testing was done, P-values were Bonferroni corrected. Statistical analyses were conducted using SPSS version 10.0. Means are given with standard errors.

## Results

Sixty-four animals were instrumented during the 7 years of study. Of these, six instruments did not transmit and another six could not be used for this study due to the nature of their duty cycle program. Seven animals had valid satellite records but did not return to Sable Island in January and therefore could not be weighed a second time to estimate mass gain. Therefore, we obtained satellite records from 52 seals (26 males and 26 females) that ranged in duration from 3 to 10 months; 12 records

beginning in May/June, and 40 in September/October. The satellite transmitters on 27 seals were not duty cycled, permitting estimates of daily locations to be used for analysis of movement. The satellite transmitters on the other 35 seals were 50% duty cycled (one day on, one day off). Thus, we calculated mean location every 2 days for the entire set of 52 satellite records.

We received 21747 locations from these 52 seals, for an average of  $5.4 \pm 0.16$  locations per day. Filtering the data eliminated 6,414 locations (29.5%) leaving 15333 useable locations (daily mean =  $3.9 \pm 0.13$ ) for our analyses (Table 1). Males had a significantly greater number of mean locations per day than females ( $5.8 \pm 0.23$  locations/d,  $5.0 \pm 0.20$  locations/d, respectively,  $t = 2.60$ ,  $df = 52$ ,  $P = 0.012$ ).

## Bi-daily movements

Of the 52 seals for which locations were calculated every second day, the trajectories of 25 animals (48.1%) fit the CRW model (Fig. 2a,b). The tracks of another 15 animals (28.8%) were overpredicted by the CRW model, and thus were classified residents. These seals had low net squared displacement ( $R_n^2$ ), and typically made short foraging trips from Sable Island (Fig. 2c,d). The remaining 12 animals (23.1%) were underpredicted by the CRW model and exhibited greater directionality of movement and longer move lengths than expected (directed movers, Fig. 2e,f).

Movement characteristics differed significantly among movement types (MANOVA Pillai's trace,  $F_{14, 88} = 6.47$ ,  $P < 0.001$ ). Based on Tukey's post hoc tests, significant differences in kernel 95% home range, mean  $R_n^2$ , sum of distances traveled, mean distance traveled, and mean speed were found among all three movement types (Table 2). Mean vector also differed significantly between CRWs and residents, and between directed movers and residents. The index of linearity differed between the residents and directed movers (Table 2). With the exception of mean move length and mean speed, the coefficients of variation (CV) for measured characteristics were high, indicating considerable individual variability within each movement type.

Table 1. Percentage of locations (n) by Argos location quality index (LQ), prior to filtering and post-filtering using the algorithm in Austin et al. (2003).

Argos LQ	Unfiltered (%)	Filtered (%)
3	3.2	4.3
2	6.2	8.1
1	11.1	14.0
0	17.5	18.6
A	23.8	23.9
B	38.2	31.1
N	21747	15333

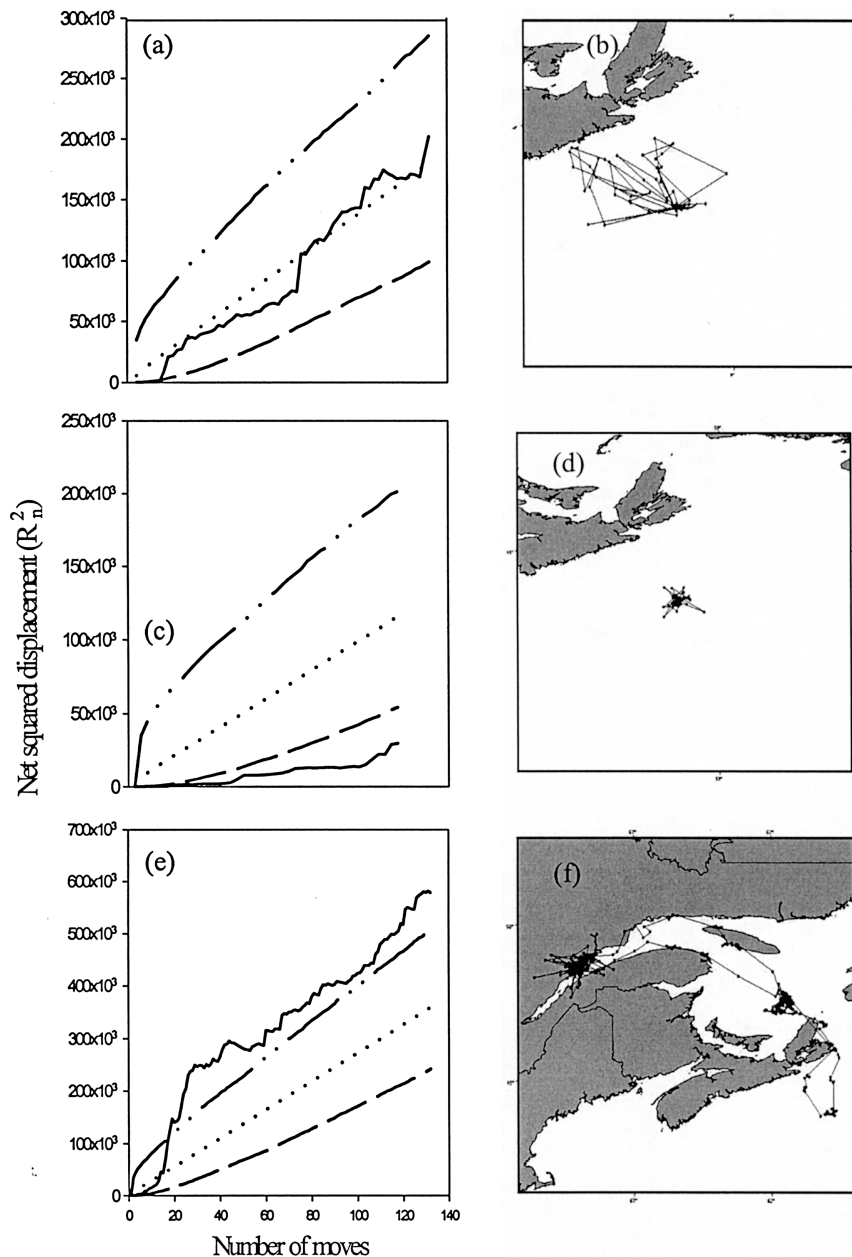


Fig. 2. Three examples of observed vs predicted  $R_n^2$  and the corresponding trajectories (a)  $R_n^2$  of seal 23, a correlated random walker, (b) satellite trajectory of seal 23. (c)  $R_n^2$  of seal 146, a resident, (d) satellite trajectory of seal 146. (e)  $R_n^2$  of seal 2986, a directed mover, (f) satellite trajectory of seal 2986. Dotted line (.....) indicates expected  $R_n^2$ , solid line (—) indicates observed  $R_n^2$ , dashed line (---) indicates lower 95% confidence interval, and dot-dash line (-·-·-) indicates upper 95% confidence interval.

Mean turning angle approached  $180^\circ$  in residents, suggesting a propensity to make successive turns which reversed the direction of movement (Table 2). In addition, only in residents did successive angles show a significant directional bias (Rayleigh's  $z = 2.95$ ,  $P < 0.05$ ). Across all animals, a significant positive ACF was found at Lag = 1, but all other lags were non-significant (Table 3). When each movement type was considered separately, a significant positive ACF was found at Lag = 1 only in CRWs and residents, whereas a

significant negative ACF was found at a Lag = 2 in directed movers (Table 3). Sequential move lengths were not autocorrelated across all animals (Pearson's  $r = 0.03$ ,  $P = 0.09$ ), however, when Pearson's correlation coefficients were calculated for each movement category, there was a significant autocorrelation in the move lengths of the directed movers (Pearson's  $r = -0.13$ ,  $P < 0.001$ ).

We next examined if sex of the animal affected movement behaviour. Males were more likely to be directed movers than females, whereas females were

Table 2. Mean movement characteristics  $\pm$ SE and coefficient of variation (CV, in parentheses) by movement type for bi-daily locations. Significant differences based on Tukey's post hoc tests.

Movement characteristic	CRW	Resident	Directed mover
Mean move length (km)	35.40 $\pm$ 1.33 <sup>a*,b*</sup> (18.8)	19.61 $\pm$ 0.96 <sup>b*,c*</sup> (18.9)	46.08 $\pm$ 2.09 <sup>a*,c*</sup> (15.8)
Total distance traveled (km)	1785.9 $\pm$ 235.7 <sup>a*,b*</sup> (66.0)	849.8 $\pm$ 96.1 <sup>b*,c*</sup> (43.8)	3452.3 $\pm$ 510.5 <sup>a*,c*</sup> (51.2)
Index of linearity	0.059 $\pm$ 0.008 (69.6)	0.088 $\pm$ 0.019 <sup>b</sup> (82.1)	0.038 $\pm$ 0.009 <sup>a</sup> (85.0)
Mean R <sub>n</sub> <sup>2</sup> (km <sup>2</sup> /h)	87796 $\pm$ 16103 <sup>a*,b*</sup> (56.8)	56511 $\pm$ 21757 <sup>b*,c*</sup> (61.3)	93438 $\pm$ 23256 <sup>a*,c*</sup> (46.0)
Mean vector (r)	0.167 $\pm$ 0.017 <sup>a</sup> (64.7)	0.211 $\pm$ 0.033 <sup>c</sup> (43.0)	0.181 $\pm$ 0.037 <sup>a</sup> (56.7)
Mean speed (km/h)	0.762 $\pm$ 0.029 <sup>a*,b*</sup> (18.71)	0.423 $\pm$ 0.021 <sup>b*,c*</sup> (18.91)	1.00 $\pm$ 0.046 <sup>a*,c*</sup> (15.93)
Mean turning angle	61.09 <sup>o</sup>	- 176.33 <sup>o</sup>	158.02 <sup>o</sup>
Kernel HR 95% (km <sup>2</sup> )	25879 $\pm$ 5068 <sup>a*,b</sup> (97.9)	3965 $\pm$ 436 <sup>b*,c*</sup> (42.6)	70680 $\pm$ 21210 <sup>a*,c</sup> (104.0)
Kernel HR 50% (km <sup>2</sup> )	3710 $\pm$ 832 (112.2)	543 $\pm$ 92 (65.8)	12564 $\pm$ 3602 (99.3)

<sup>a</sup> significantly different from residents at  $P \leq 0.05$ .

<sup>b</sup> significantly different from directed movers at  $P \leq 0.05$ .

<sup>c</sup> significantly different from CRWs at  $P \leq 0.05$ .

\* indicates significance at  $P < 0.001$ .

Table 3. Autocorrelation Function (ACF) of turning angles for each movement type for up to 6 successive lags for bi-daily locations (n = 52), with  $\pm$ SE. Significant ACFs are indicated with an \*.

Lag	CRW	Resident	Directed mover	All seals
1	0.17 $\pm$ 0.032*	0.101 $\pm$ 0.039*	0.020 $\pm$ 0.035	0.11 $\pm$ 0.022*
2	- 0.047 $\pm$ 0.038	- 0.024 $\pm$ 0.049	- 0.071 $\pm$ 0.031*	- 0.035 $\pm$ 0.026
3	- 0.064 $\pm$ 0.036	- 0.051 $\pm$ 0.027	0.043 $\pm$ 0.026	- 0.040 $\pm$ 0.021
4	- 0.0064 $\pm$ 0.037	0.0024 $\pm$ 0.058	0.011 $\pm$ 0.045	0.0020 $\pm$ 0.026
5	- 0.015 $\pm$ 0.032	0.047 $\pm$ 0.046	0.020 $\pm$ 0.060	0.010 $\pm$ 0.022
6	- 0.034 $\pm$ 0.038	0.066 $\pm$ 0.054	0.010 $\pm$ 0.037	0.014 $\pm$ 0.027

more likely to be residents (likelihood ratio = 7.43, df = 2,  $P = 0.024$ , Table 4). A consequence of this difference was that the 95% kernel home range size of males was significantly larger than females  $F_{1,50} = 17.44$ ,  $P < 0.001$ , Table 4). Similarly, mean distance traveled between locations was significantly greater in males than in females ( $F_{1,50} = 12.21$ ,  $P < 0.001$ ), as was mean speed ( $F_{1,50} = 12.01$ ,  $P < 0.001$ ).

The probability of exhibiting a particular movement pattern also differed by the season of instrument deployment. Animals instrumented in spring were

more likely to be directed movers, whereas animals instrumented in autumn were more likely to be residents or CRWs (likelihood ratio = 11.64, df = 2,  $P = 0.003$ ). The mean 95% kernel home range size of seals whose record began in spring ( $41029 \pm 12413$  km<sup>2</sup>) was greater than those instrumented in the fall ( $26909 \pm 7266$  km<sup>2</sup>), although this difference was not significant. Mean move length was significantly greater in seals instrumented in spring ( $42.5 \pm 3.4$  km) than in fall ( $30.8 \pm 1.6$  km;  $F_{1,50} = 8.17$ ,  $P = 0.006$ ), as was linearity index (spring:  $0.046 \pm 0.013$ , fall:  $0.067 \pm 0.008$ ;  $F_{1,50} = 3.87$ ,  $P = 0.05$ )

Table 4. Number of male and female grey seals by movement type and mean movement characteristics  $\pm$ SE based on bi-daily locations. Significance as determined from a oneway GLM at  $P \leq 0.05$  denoted with an \*.

Movement type	Males (n = 25)	Females (n = 27)
CRW	14	11
Resident*	3	12
Directed mover*	8	4
95% kernel home range (km <sup>2</sup> )*	45814 $\pm$ 11249	15157 $\pm$ 4944
50% kernel home range (km <sup>2</sup> )	7725 $\pm$ 1933	2169 $\pm$ 854
Mean distance traveled (km)*	38.39 $\pm$ 1.93	28.61 $\pm$ 2.14
Total distance traveled (km)	2171.0 $\pm$ 292.1	1650.0 $\pm$ 294.1
Mean R <sub>n</sub> <sup>2</sup> (km <sup>2</sup> /h)	94783 $\pm$ 14235	66573 $\pm$ 17155
Mean speed (km/h)*	0.83 $\pm$ 0.042	0.62 $\pm$ 0.047

and mean  $R_n^2$  (spring:  $197166 \pm 29593$ , fall:  $48737 \pm 5582$ ;  $F_{1,50} = 24.59$ ,  $P < 0.001$ ).

Although all of our study seals were adults (mean =  $18.2 \pm 0.9$  yr), ages ranged from 8 to 28 years. Males in the study were significantly older than females ( $20.8 \pm 1.2$  yr,  $16.4 \pm 1.2$  yr, respectively;  $t_{50} = 2.85$ ,  $P = 0.006$ ). As foraging and thus movement behaviour might be affected by experience, we divided our sample into two groups based on the median age of 18. We found that older seals were more likely to be CRWs, whereas younger seals were more likely to be residents. Both older and younger seals were equally likely to be directed movers (likelihood ratio = 10.72,  $df = 2$ ,  $P = 0.005$ ). Using a univariate GLM with age class as a factor, 95% kernel home range size was significantly greater in older ( $40859 \pm 10488$  km<sup>2</sup>) vs younger animals ( $18056 \pm 5959$  km<sup>2</sup>;  $F_{1,50} = 4.12$ ,  $P = 0.05$ ,  $R^2 = 0.076$ ). The low  $R^2$  value indicates that only a small amount of the variation can be accounted for by age, and thus may not be a biologically significant factor.

Neither body mass at deployment nor rate of mass gain from deployment to recapture differed among movement types ( $F_{2,49} = 1.95$ ,  $P = 0.15$ ;  $F_{2,28} = 1.98$ ,  $P = 0.16$ , Table 5).

### Daily movements

Of the 27 seals located daily, 17 were CRWs (63.0%), 7 were residents (25.9%) and 3 were directed movers (18.5%). At this scale there were proportionately more CRWs and fewer directed movers and residents. The movement type of 6 out of 27 animals (22.2%) changed when they were modeled at daily rather than bi-daily temporal scale, suggesting that movement type may be scale dependent. Five animals that had been classified as residents using bi-daily data were classified as CRWs using daily locations, whereas one CRW was reclassified as a directed mover.

Kernel home range sizes estimated using mean daily locations did not differ significantly from those estimated using bi-daily locations (paired t-test,  $t_{26} = -2.09$ ,  $P > 0.05$ , Bonferroni corrected), nor did mean vector (paired t-test,  $t_{26} = 0.15$ ,  $P > 0.05$ , Table 6). However, linearity (paired t-test,  $t_{26} = -4.51$ ,  $P < 0.001$ ) was significantly greater for the bi-daily data. This was presumably because more of the tortuosity in the trajectory was captured at shorter time scales. Both

Table 5. Mean body mass at deployment and rate of mass change by day for each movement type.

Movement type	Mass at deployment (kg)	Rate of mass change per day (kg d <sup>-1</sup> )
CRW	$201.24 \pm 8.14$	$0.56 \pm 0.06$
Resident	$176.83 \pm 7.58$	$0.53 \pm 0.13$
Directed mover	$182.70 \pm 12.09$	$0.57 \pm 0.09$

Table 6. Mean movement characteristics  $\pm$  SE of 27 seals sampled bi-daily and daily. Significant differences based on paired t-tests at  $P \leq 0.05$  (Bonferroni corrected) are denoted with an \*.

Movement characteristic	Bi-daily locations	Daily locations
Mean move length (km)*	$29.1 \pm 2.2$	$24.7 \pm 1.9$
Total distance traveled (km)*	$1163.4 \pm 143.6$	$1755.0 \pm 174.3$
Index of linearity*	$0.082 \pm 2.21$	$0.027 \pm 0.01$
Mean $R_n^2$ (km <sup>2</sup> /h)*	$39050 \pm 8130$	$55229 \pm 9522$
Mean vector (r)	$0.20 \pm 0.02$	$0.21 \pm 0.02$
Kernel HR 95% (km <sup>2</sup> )	$25987 \pm 10223$	$23976 \pm 9133$
Kernel HR 50% (km <sup>2</sup> )	$3753 \pm 1458$	$3395 \pm 1347$

cumulative distance traveled (paired t-tests,  $t_{26} = -10.89$ ,  $P < 0.001$ ) and mean  $R_n^2$  (paired t-test,  $t_{26} = 5.07$ ,  $P < 0.001$ ) were significantly greater at the shorter time scale (Table 6).

The mean turning angle was  $32.0^\circ$  for CRWs,  $167.3^\circ$  for residents and  $114.0^\circ$  for directed movers. Both the residents and directed movers showed a propensity for turning in a particular direction (residents: Rayleigh's  $z = 6.31$ ,  $P < 0.05$ ; directed movers: Rayleigh's  $z = 0.71$ ,  $P < 0.05$ ). Examining the ACF for the mean daily locations across all non-duty cycled animals indicated a significant positive correlation at a lag = 1 (Table 7), and a significant negative correlation at lags = 3 and 4. Across all three movement types, there was a significant positive ACF at lag = 1. However, there was a significant negative ACF for the residents at lags = 3 and 6. Directed movers had a significant negative ACF at lag = 5 and a significant positive ACF at lag = 6 (Table 7).

Using the daily locations, again males had larger kernel 95% home ranges than females (males:  $39781 \pm 16726$  km<sup>2</sup>, females:  $6956 \pm 1552$  km<sup>2</sup>;  $F_{1,25} = 9.75$ ,  $P = 0.004$ ,  $R_2 = 0.28$ ). Similarly, a one-way GLM with age class as a factor and 95% kernel home range as a dependent factor showed that kernel home range was significantly greater in older animals ( $40917 \pm 16590$  km<sup>2</sup>) than in younger animals ( $5731 \pm 887$  km<sup>2</sup>;  $F_{1,25} = 7.18$ ,  $P = 0.013$ ,  $R^2 = 0.22$ ).

### Lévy flight

The CRW model fit the observed trajectories of approximately half of all seals studied. An examination of the distribution of move lengths suggested that a Lévy flight might also be an appropriate model. However, only 8 of the 52 seals (15.3%), had frequency distributions of movement lengths that fit the negative power law distribution of a Lévy flight; indicating that long movements occurred more often than expected if the distribution of movement lengths was normal (Marell et al. 2002). Five of the animals that fit the Lévy distribution



Table 7. Autocorrelation function (ACF) of turning angles for each movement type for up to 6 successive lags for mean daily locations ( $n = 27$ ), with  $\pm$ SE. Significant ACFs are indicated with an \*.

Lag	CRW	Resident	Directed mover	All seals
1	0.099 $\pm$ 0.029*	0.142 $\pm$ 0.037*	0.105 $\pm$ 0.016*	0.12 $\pm$ 0.013*
2	-0.0042 $\pm$ 0.034	-0.0035 $\pm$ 0.034	-0.026 $\pm$ 0.092	-0.011 $\pm$ 0.007
3	-0.010 $\pm$ 0.044	-0.075 $\pm$ 0.024*	-0.071 $\pm$ 0.054	-0.052 $\pm$ 0.021*
4	-0.070 $\pm$ 0.036	-0.075 $\pm$ 0.040	-0.051 $\pm$ 0.053	-0.065 $\pm$ 0.007*
5	0.0094 $\pm$ 0.032	-0.029 $\pm$ 0.035	-0.077 $\pm$ 0.034*	-0.032 $\pm$ 0.025
6	-0.0081 $\pm$ 0.038	-0.056 $\pm$ 0.025*	0.068 $\pm$ 0.029*	0.0020 $\pm$ 0.036

also fit the CRW model, whereas the other three animals were residents.

To investigate if the temporal scale of sampling affected the number of seal trajectories fit by the Lévy model, we repeated the analysis using the daily sampled seals. In this sample, 9 of the 27 animals, or 33.0% of trajectories fit a Lévy flight (Fig. 3). Of these, 4 were males and 5 were females but there is no evidence that one sex is more likely to fit a Lévy flight than another (log-likelihood ratio = 0.30,  $df = 1$ ,  $P = 0.59$ ). Of the animals that fit the Lévy flight distribution, 5 were CRWs and 4 were residents, but no one movement type was more likely to fit the Lévy flight (log-likelihood ratio = 4.21,  $df = 2$ ,  $P = 0.122$ ). None of the seals classified as directed movers fit the Lévy flight distribution. Directed movers had a frequency distribution characterized by more long move lengths than short ones, resulting in a distribution with no descending right tail.

### Distance from Sable Island

Although the analysis of the movement trajectories using quantitative models provided considerable insight into how animals use space, it did not capture all aspects of movement. Since all seals began their trajectory at the same location, the mean distance from Sable Island provided another way to quantify movement behaviour over the course of the trajectory. Distance from Sable Island over time varied significantly among movement types, with the average distance being greatest in directed movers (258.8  $\pm$  59.6 km), least in residents (38.8  $\pm$  39.7 km) and intermediate in CRWs (90.7  $\pm$  7.3 km, Kruskal-Wallis  $\chi^2 = 31.34$ ,  $df = 2$ ,  $P < 0.001$ ).

The way in which distance from Sable changed over the course of the trajectory provided insight into the structure of foraging trips (Fig. 4a-f). Directed movers made one long trip from Sable Island, whereas residents undertook many short trips. Directed movers may have used other haul-out areas other than Sable Island and hence we did not calculate trip statistics for this group of animals. Mean trip duration from Sable Island in residents (6.8  $\pm$  0.78 d;  $CV = 103.2$ ) was significantly less than that of CRWs (10.6  $\pm$  0.11 d,  $CV = 91$ ;  $t_{225} = 4.04$ ,  $P < 0.001$ ). Residents also spent a lower percentage

of time away from Sable (i.e. outside the 20 km box) than CRWs (33.4  $\pm$  3.6% d and 53.9  $\pm$  3.9% d, respectively;  $t_{38} = 3.5$ ,  $P = 0.001$ ). Plots of travel speed over time demonstrated that high speeds were typically associated with rapidly changing distance from Sable (Fig. 4).

### Discussion

The correlated random walk model did not describe the movement behaviour of over half the grey seals in this study. However, testing the trajectories of individual seals against predictions of the CRW model provided a useful way to differentiate among types of movement: (1) those which moved in a random fashion, the CRWs, (2) those whose movement patterns were characterized by short return trips from a single place, the residents, and (3) those seals which undertook long distance, directed movements away from the island, only returning to the island just prior to the breeding season, the directed movers. Most animals did not fit the Lévy flight, which indicates that other search tactics are involved, and that prey items consumed by grey seals are not randomly distributed. Our results also show that there is considerable individual variability within each of the three movement types (i.e. high CVs), with movement tactics seemingly varying along a continuum from short, localized trips to distant, extended trips.

Our primary goal here was not to estimate the proportion of each movement type within the population. Nevertheless, we identified several factors that will affect such estimation. Directed movers were more likely among seals tagged after the spring molt, whereas residents were more common among seals tagged in the fall, suggesting that there may be seasonal changes in the proportion of movement types used by grey seals. Or, alternatively, directed movers may simply spend less time on Sable Island in the fall and thus are less available to capture than seals exhibiting other movement types. Sex of the animal also affected the proportion of movement types. Male and female grey seals exhibit different seasonal patterns of body mass and energy storage (Beck et al. 2003) and diving behaviour (Beck et al. 2003a, b) and as a result may use different search tactics. Finally, the frequency of sampling location affected our perception of the proportion of seals exhibiting different

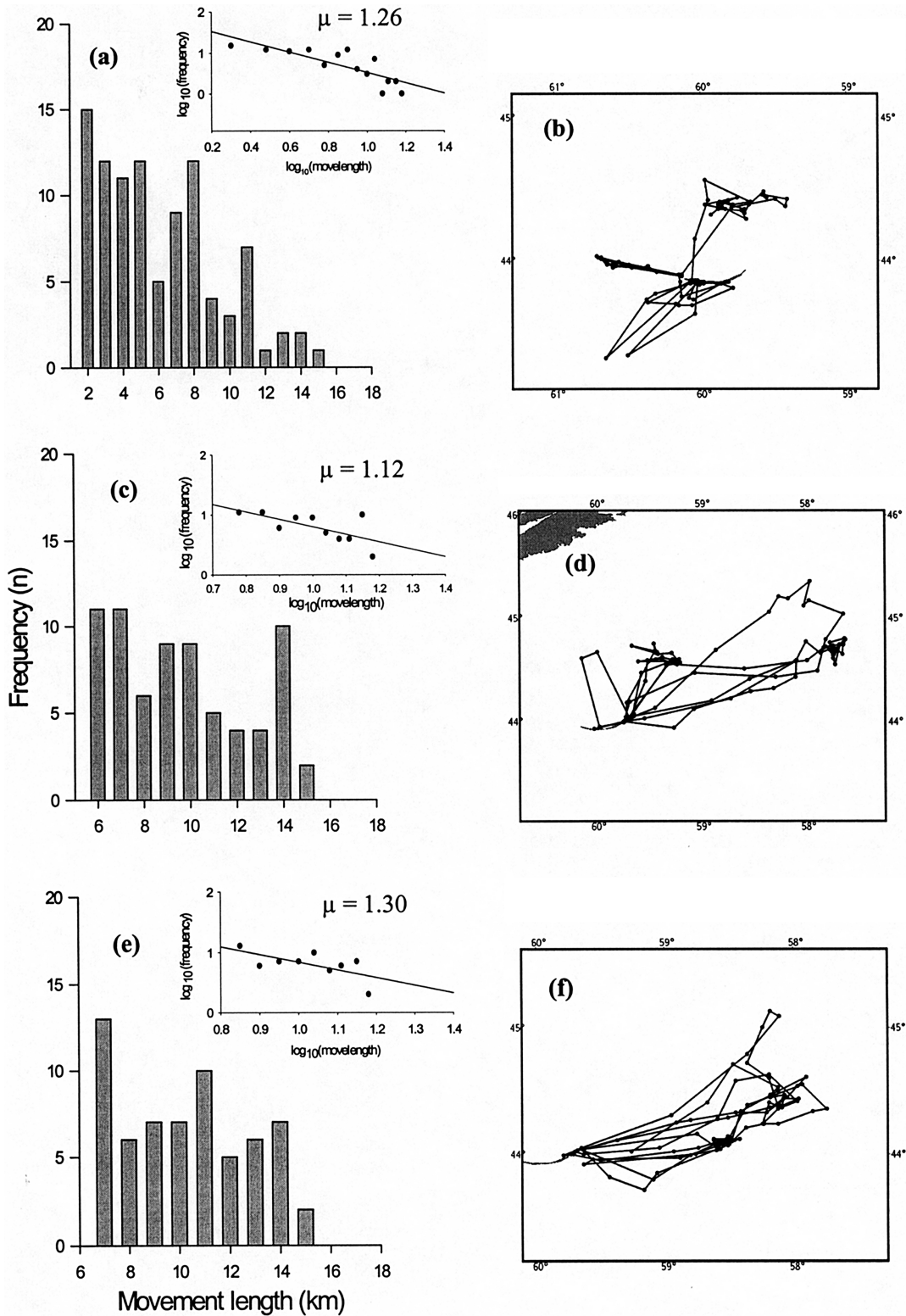


Fig. 3. Average frequency distribution of movement lengths for each three seals which fit the Lévy distribution. (a) seal 6118, a resident, (b) seal 6124, a CRW and (c) seal 6125, a CRW. Inserted is a double-log plot of the same data fitted with a regression line, where  $\mu$  is the power-law exponent of the frequency distribution. Lévy flights follow a distribution of  $1 < \mu \leq 3$ .

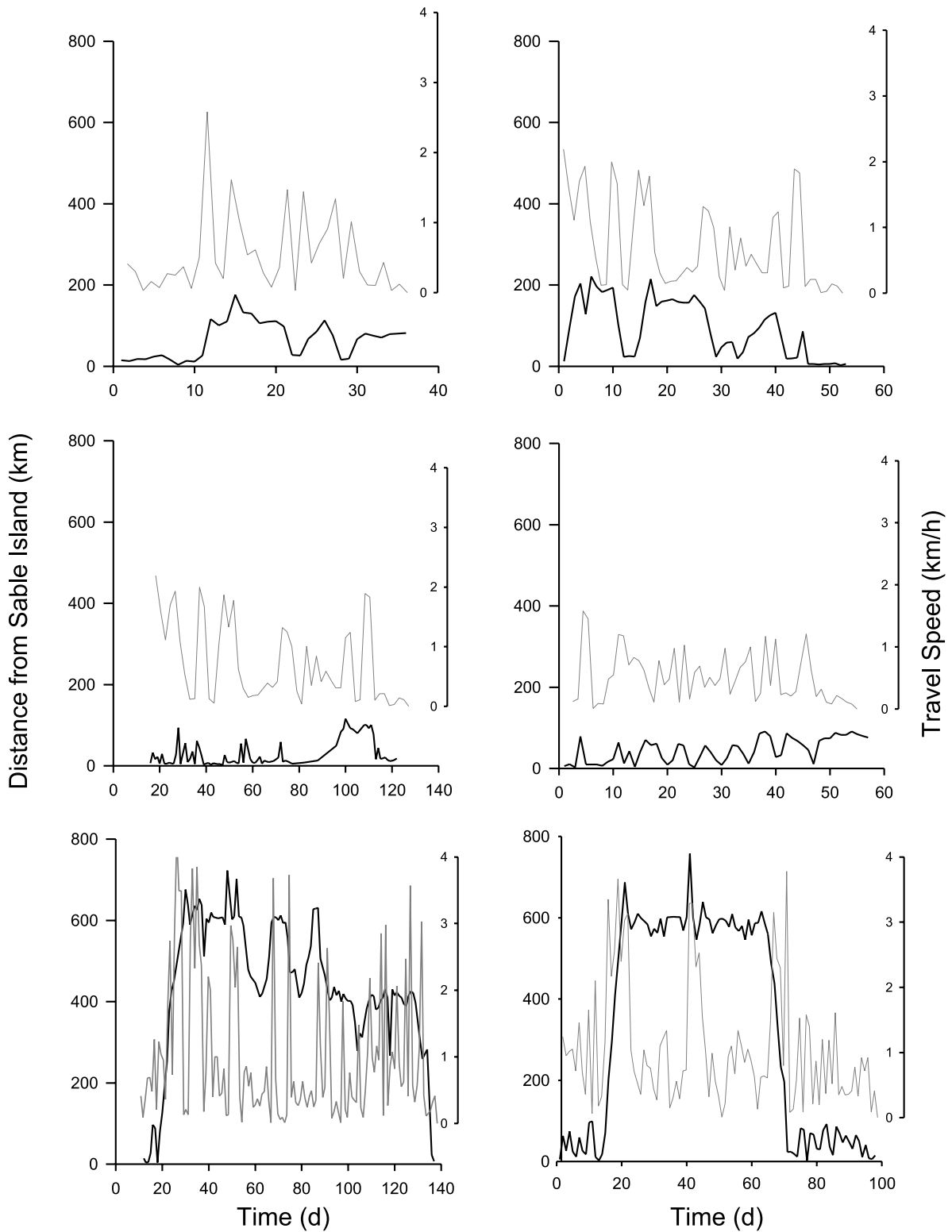


Fig. 4. Distance (km) from Sable Island over time (solid black line) and travel speed over time (solid grey line) for 6 seals. (a) female 24, a CRW. (b) male 3099, a CRW. (c) female 2999, a resident. (d) male 6115, a resident. (e) female 3616, a directed mover. (f) male 3662, directed mover.

movement tactics (e.g. the proportion fitting a Lévy flight).

An examination of the assumptions of the CRW model may indicate why some animals failed to meet the predictions of the model. The two key assumptions of a CRW are that move lengths and turning angles are not serially autocorrelated. Such autocorrelation in move lengths is the primary reason for rejection of CRW models (Turchin 1998). Move lengths were strongly autocorrelated in directed movers indicating that the distance traveled at  $t_1$  is a function of the distance traveled at  $t_1 - 1$ . As a result, the majority of move lengths in the directed movers were of similar size. Furthermore, the distribution of move lengths in the directed movers tended to be strongly biased towards longer move lengths, with the mean distance traveled considerably greater than that seen in the CRWs and residents. Long move lengths are generally associated with traveling, whereas shorter move lengths are characteristic of foraging behaviour (Pyke 1978, Stanton 1982). Therefore, by using many long, similarly sized move lengths, directed movers reduce travel time to distant feeding areas. Mean travel speed of directed movers (Fig. 4) was also higher than that of residents and CRWs. A number of studies suggest that foraging speed varies as a function of the distance between patches (Spalinger et al. 1988, Speakman and Bryant 1993, Shipley et al. 1996), such that as distance increases so should optimal speed. According to optimal foraging theory (OFT), animals should attempt to minimize time spent between patches in favour of time spent within patches (Pyke 1978). Long-distance travel should only be taken if there is a high probability of reward from the distant patch. In all cases, the destination of the directed movers in our sample was a known offshore or coastal area of high prey abundance. For example, seal 2986 (Fig. 2c) moved quickly to an area of the St. Lawrence Estuary known to contain a productive upwelling, used by other marine mammals (Simard and Lavoie 1999). Although we could not determine the quality of prey patches directly, we can assume that these were areas of high quality given that these animals returned to the Sable Island having gained sufficient reserves to withstand prolonged fasting period associated with the breeding season.

The second reason for failing to fit a CRW is the autocorrelation of turning angles. Turning angles were significantly positively correlated at a time lag = 1 across all animals, and for residents, CRWs, and directed movers (daily locations only), indicating the propensity to make sequential turns in the same direction from one move to the next, also known as directional persistence or directional bias. While perfectly correlated angles result in a straight trajectory, in general, positive autocorrelation of turning angles will result in a more tortuous trajectory (Zollner and Lima 1999), thereby

lowering the overall net squared displacement. This is generally characteristic in areas where animals may be foraging (Bovet and Benhamou 1991).

In addition to testing first order autocorrelations at a lag = 1, we also examined higher-order autocorrelations up to lag = 6 (Turchin 1998). Most lags > 1 had autocorrelations that were negative in all three movement types, indicating the tendency to turn in opposite directions, particularly observed in the residents. As expected, residents chose turning angles which approach  $180^\circ$  at both the bi-daily and daily temporal scales. In this manner, an individual tends to reverse its direction ensuring that it remains within the vicinity of Sable Island, thereby reducing the probability of leaving the habitat.

There may be several reasons for residents to forage near Sable Island. First, proximity to a haul-out site has a suite of potential advantages. Hauling out on land may be necessary for rest, to engage in social interaction and to reduce risk of predation from killer whales (*Orcinus orca*) and white sharks (*Carcharodon carcharias*). McConnell et al. (1999) found that, in the North Sea, most foraging by grey seals apparently occurred in close proximity to haul-out sites. Second, Sable Island Bank is a relatively shallow (50–100 m), sandy region, which is habitat for a number of important grey seal prey, such as sandlance (*Ammodytes dubius*) and capelin (*Mallotus villosus*, Beck 2002). Thus, by remaining near Sable Island, travel costs to prey patches are minimized.

In contrast, mean turning angle of the CRWs is closer to  $0^\circ$ , and distribution of turning angles is not significantly clustered around any given direction. Generally, a normal distribution of turning angles suggests that an animal's movement pattern is random (Levin et al. 1971). In the seals for which we have daily movements, we found a significant negative autocorrelation for the residents at a lag = 3 and a lag = 6. This indicates some long-term memory in movement behaviour, although this effect is not as strongly correlated as at a lag = 1 and consequently has less influence (Turchin 1998). The longest-term autocorrelations are seen in the directed movers (daily trajectories lag = 5 and lag = 6) as would be expected of animals exhibiting long distance, directed travel, indicating memory in the direction of movement.

Within the context of OFT, optimal directionality in an animal's trajectory should lead to a decrease in the number of patches revisited and increase the possibility of encountering new patches (Wolf and Hainsworth 1990). The "lost opportunity principle" refers to the revisitation of already exploited patches; by doing so, an animal loses the opportunity to seek out other patches where resource availability is higher (Stephens and Krebs 1986). Zollner and Lima (1999) found through simulation that the best search tactic to avoid "lost opportunities" is to use non-systematic search trajectories that are nearly straight, with optimal angular concentration

being  $>0.9$ . Nevertheless, we found a relatively low angular concentration (mean vector) of our animals of  $0.19 \pm 0.02$ , also reported in foraging swans (*Cygnus columbianus bewickii*, Nolet and Mooij 2002) and caribou (*Rangifer tarandus*, Bergman et al. 2000). Zollner and Lima (1999) concluded that when food patches are clumped, the optimal angular concentration does not matter, provided the trajectory is neither perfectly straight nor random. We know from studies of the diving patterns of grey seals that the preferred foraging depth is 50–100 m (Beck et al. 2003a). In the Northwest Atlantic, distribution of shallow offshore banks in the 50–100 m depth range is not uniform, rather they tend to be clumped across the Scotian Shelf, particularly in the area surrounding Sable Island (Fig. 1). This may account for the low angular concentration observed in grey seals.

According to existing theory, the probability of successful dispersal across a habitat is increased by employing a strongly correlated random walk (Zollner and Lima 1999). Nonetheless, our results show that only about half of the adult grey seals studied fit the CRW model. Another type of random walk, the Lévy flight, also predicted the movement of about a third of grey seals whose location was sampled daily. A Lévy flight search tactic is advantageous when resources are randomly distributed because the probability of returning to a previously visited site is smaller than for a normal distribution (Viswanathan et al. 1999). In addition, a Lévy distribution is preferable because the number of new sites visited is greater than for simple random walkers under typical Brownian motion (Klafter et al. 1996). Thus, our results suggest that some grey seals do not use random search tactics to locate prey patches. We suggest that both the clumped distribution of foraging habitats and many years of foraging experience in these adult grey seals may account for our results.

Age was a significant predictor of movement type and home range size (this study), as well as aspects of diving behaviour (Beck et al. 2003a) Swingland et al. (1989) found that the proportion of migratory and sedentary tortoises (*Geochelone gigantea*) varies with age, with young, immature animals appearing inconsistent in their movement patterns, and older animals being more likely to migrate. Grey seals are long lived, and adults certainly will have had many years for foraging experience to learn the location of profitable prey patches. This could explain the rapid direct movements of directed movers to distant areas followed by a subsequent change in search behaviour (Fig. 4). The younger animals in our study were more likely to exhibit movements characteristic of residents, whereas older animals were more likely to display a random search or directed travel pattern. Nevertheless, age explained relatively little of the variation in movement type and so the biological significance of this difference remains unclear.

Differences in diet preferences or dietary requirements among individuals might also affect movement patterns to the extent that prey distributions differ in time and space. For example, the distribution of some important grey seal prey, such as capelin and sand lance, are highly clumped in time and space over shallow and sandy habitats (Scott and Scott 1988). However, other important prey items such as flounders and other flatfish (Beck 2002) tend to have a more uniform distribution at the scale of the offshore banks shown in Fig. 1 (Groundfish Survey Database, Department of Fisheries and Oceans, Canada). It is likely that the costs and gross amounts of food consumed in order to reach similar levels of energy storage vary between individuals, and this difference will be reflected in prey selection. Indeed, by examining diet at an individual level using techniques such as fatty acid signature analysis (Iverson et al. 1997), in future we will be able to link seal movement and prey distribution in these animals.

Variation in movement tactics within a population have been observed in other taxa. For example in the cane toads, *Bufo marinus*, some individuals are nomadic, while others remain in a single small area for most of their existence (Schwarzkopf and Alford 2002). Among birds, many species show distinct migratory and sedentary behavioural morphs, known as partial migration. For example, in goshawks (*Accipiter gentiles*) and the chaffinch (*Fringilla coelebs*), the proportion of migrants in the population fluctuates, likely as a result of changing food conditions, and is related to the sex or age of the individual (Newton 1979). Variation in movement behaviour has also been observed in ungulate populations. For example, within the same habitat in northern Sweden, half of a population of moose (*Alces alces*) migrated while the other half remained sedentary (Ball et al. 2001), similar to the behavioural variation exhibited by the seals in this study.

Swingland and Lessells (1979) suggest that migrant and non-migrant individuals will persist in a population if they receive approximately equal pay-offs. We found no difference in amount of mass gained by grey seals among the three movement types, indicating that each of these are successful search tactics. Furthermore, 20 of the 27 study females (74%) returned to Sable Island, gave birth, and nursed healthy pups. Among these 27 females reproductive success was independent of movement type (log-likelihood ratio = 1.27,  $P = 0.53$ ). We could not conduct a similar analysis in males because we did not have a reasonable measure of the reproductive success of the study seals.

Sex-specific foraging behaviour has been found in several taxa (Pérez-Barbería and Gordon 1999, Le Boeuf et al. 2000, Jormalainen et al. 2001, Ishikawa and Watanuki 2002), including grey seals (Beck et al. 2003a, b). Male and female grey seals exhibited different seasonal patterns of diving at several temporal scales,

with males generally diving deeper, but with less overall dive effort (shorter dives with less time at depth). There is also evidence that males consume a lower energy density diet than females (Beck 2002). Therefore it is not entirely surprising that males and females also differ in the way in which they search for food. Females show a greater tendency to remain in the vicinity of Sable Island as residents, and use a smaller home range size, while males exhibit more long distance travel, and as a result have significantly greater home range sizes. By using a larger foraging range, males presumably encounter a greater diversity of prey species. This coupled with their larger body size (males are 1.5 times heavier than females) may enable males to process larger quantities of lower quality prey (Beck 2002). Consequently, males may be more efficient predators than females, spending less time foraging despite their larger size and absolute energy requirement, a dichotomy also observed in ungulates (Ginnett and Demment 1997, Ruckstuhl 1998, Pérez-Barbería and Gordon 1999).

Although there is evidence of sex-differences in the proportions of movement types exhibited by grey seals, nevertheless, both sexes used all three search tactics. Thus, there remains a great deal of individual variability in the movement patterns in this population of grey seals (this study), as well as in the North Sea (McConnell et al. 1992) and in the Baltic Sea populations (Sjöberg and Ball 2000). In addition there is a considerable amount of variation in movement patterns between populations. Some of this variation is captured in estimates of kernel home ranges. For example, the mean 95% kernel home range of Baltic seals ( $2658 \pm 508 \text{ km}^2$ ) is significantly less than that in this study ( $23976 \pm 9133 \text{ km}^2$ ,  $t = -4.17$ ,  $df = 36$ ,  $P < 0.001$ ; Sjöberg and Ball 2000).

This difference seems to reflect the greater complexity of the continental shelf habitat used by grey seals in the northwest Atlantic compared to the relatively uniform and shallow Baltic Sea. Ungulates also show differences in home range size between populations (Lesage et al. 2000), seemingly as a result of density-dependent competition (Nelson and Mech 1984) and habitat differences (Lincoln 1992).

The ability to predict the population distribution and spread through the environment has important consequences for modeling resource and habitat use (Bergman et al. 2000). Understanding individual variability in movement patterns of grey seals will improve existing models of predation (Mohn and Bowen 1996) by permitting more spatially explicit estimates of predation mortality on prey populations.

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