Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging

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Summary

1. Broad-scale telemetry studies have greatly improved our understanding of the ranging patterns and habitat-use of many large vertebrates. However, there often remains considerable uncertainty over the function of different areas or the factors influencing habitat selection. Further insights into these processes can be obtained through analyses of finer scale movement patterns. For example, search behaviour may be modified in response to prey distribution and abundance.

2. In this study, quantitative analysis techniques are applied to the movements of bottlenose dolphins, recorded from land using a theodolite, to increase our understanding of their foraging strategies. Movements were modelled as a correlated random walk (CRW) and a biased random walk (BRW) to identify movement types and using a first-passage time (FPT) approach, which quantifies the time allocated to different areas and identifies the location and spatial scale of intensive search effort.

3. Only a quarter of the tracks were classed as CRW movement. Turning angle and directionality appeared to be key factors in determining the type of movement adopted. A high degree of overlap in search effort between separate movement paths indicated that there were small key sites (0·3 km radius) within the study area (4 km^2). Foraging behaviour occurred mainly within these intensive search areas, indicating that they were feeding sites.

4. This approach provides a quantitative method of identifying important foraging areas and their spatial scale. Such techniques could be applied to movement paths for a variety of species derived from telemetry studies and increase our understanding of their foraging strategies.

Key-words: correlated random walk, first-passage time, search paths, spatial scale.

Introduction

Broad-scale telemetry studies have greatly improved our understanding of the ranging patterns and habitat-use of many large vertebrates (Wiig, Born & Pedersen 2003; Baumgartner & Mate 2005). However, there often remains considerable uncertainty over the function of different areas or the factors influencing habitat selection. Further insights into these processes can be obtained through analyses of finer-scale movement patterns. For example, animals influence their encounter rates with

prey by modifying search behaviour in response to food distribution and abundance (Hill, Burrows & Hughes 2003; Biesinger & Haefner 2005). Within the marine environment, prey are often distributed in patches (Boyd 1996) and predators can take advantage of the spatial autocorrelation of prey density by using area-restricted search behaviours (Dixon 1959; Kareiva & Odell 1987; Wolf & Hainsworth 1990). Animals may intensify search effort within a prey patch by lowering speed and increasing turning rate. In areas of poorer food quality an extensive search mode is expected, where rapid, straight-line travel minimizes the time spent between patches and reduces search redundancy (Zollner & Lima 1999). Consequently, perception of food quality can dictate directly which mode of search behaviour is employed, and has an important effect on the movement patterns of animals (Fortin 2003).

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The relationship between search patterns and the distribution of food has rarely been documented for large free-ranging animals (Ward & Saltz 1994; Mårell, Ball & Hofgaard 2002). In marine systems, the spatial distribution of fish prey is poorly known at small temporal and spatial scales, making comparison between predator search effort and prey density extremely difficult. Marine predators also mainly forage beneath the surface, so that observations of feeding are rare (Heithaus *et al.* 2002). Quantitative analysis of movement paths can therefore provide an important technique to overcome these challenges and improve our understanding of the foraging strategies of marine predators.

The increasing use of radio and satellite telemetry has resulted in a rapid rise in the amount of movement data available (Hays *et al.* 2003; Wilson *et al.* 2005), but analysis techniques have developed more slowly. Studies of marine mammal movements have been largely descriptive or involved single measures such as distance travelled or swimming speed (McConnell *et al.* 1999; Whitehead & Rendell 2004). An alternative approach is a correlated random walk model (CRW). Predicted moves are determined by a random selection from empirical distributions of move lengths and turning angles. The preference for an animal to move in the direction of its head is accounted for by assuming a distribution of turning angles centred around 0° (Turchin 1998). Deviations from this model can provide insights into the search strategy adopted (Ward & Saltz 1994). For example, significant differences in speed and move length were found between grey seal trajectories fitting and deviating from a CRW (Austin, Bowen & McMillan 2004).

Animals not only make decisions about their foraging path, but also how long to stay within each patch. The time allocated to an area should provide an indication of the profitability of the patch and the trade-off between diminishing returns and the cost of finding another prey patch (Pyke, Pulliam & Charnov 1977). This time allocation can be measured using first-passage time (FPT) (Johnson, Milne & Wiens 1992). Fauchald & Tveraa (2003) extended this technique so that the spatial scale and location of concentrated search effort could be determined. This has been applied recently to the paths of foraging albatrosses, in which 85% of these exhibited an area-restricted search pattern and scale-dependent adjustments were made in relation to environmental features (Pinaud & Weimerskirch 2005). However, data obtained from satellite transmitters generally provide data on relatively coarse spatial (several kilometres) and temporal scales (generally less than seven localizations per day). This will prevent adjustments made at finer scales being identified. In this paper, movement pattern models will be applied to the tracks of bottlenose dolphins (*Tursiops truncatus* Montagu), derived from land-based theodolite surveys that record accurately the animals' fine-scale position.

Within their home range, predators are known to exhibit differential habitat use (Ingram & Rogan 2002).

In the inner Moray Firth (Scotland), sightings of bottlenose dolphins were concentrated in three small regions, suggesting that these may be important foraging areas (Wilson, Thompson & Hammond 1997). However, these areas are all narrow channels so it remains possible that they could be acting as bottlenecks, aggregating the animals and inflating the sighting rate. Thus, these areas may not provide critical habitat, but simply a passageway to other favourable sites. If this is the case, one would expect directed travel behaviour through the channel. In contrast, if these areas are important for foraging, movements are likely to be characterized by convoluted tracks indicative of searching behaviour. Analyses of dolphin movement paths can therefore provide additional insight into the function of these areas.

The objectives of this study were to use the fine-scale trajectories of bottlenose dolphins within one of these channels to establish whether the area was a preferred site for foraging or a bottleneck. The applicability of a CRW model was examined to test if the dolphins were moving randomly. FPT analysis was used to measure time allocation in different areas and to determine whether foraging behaviours occurred primarily within the intensively searched areas.

Materials and methods

DATA COLLECTION

Land-based surveys were conducted from a vantage point overlooking the entrance to the Inverness Firth (57°35′ N, 4°06′ W) (Fig. 1) at a height of approximately 86·8 m above sea level (Bailey & Lusseau 2004). Surveys occurred during May–September 2003 and May–July 2004, over all tidal states. Movement paths of the dolphins were measured using a theodolite (Leica T460, Heerbrugg, Switzerland) which measured horizontal and vertical angles. Together with knowledge of the height of the theodolite above sea level, this allowed accurate positions of the animals to be obtained (Würsig, Cipriano & Würsig 1991). The theodolite was calibrated by acquiring readings simultaneously from the theodolite and a differential global positioning system (DGPS) unit (Garmin GBR 23, Hampshire, UK), accurate to within 2 m, from positions throughout the study area up to 3·5 km from the observation site. The mean error in these locations estimated by the theodolite was 20·4 m ($N = 34$, SD = 9·19 m) and increased from 14·5 m at 0·5–1·0 km from the theodolite to 24·5 m at 3·0–3·5 km.

Focal group follows were performed during the surveys (Altmann 1974; Mann 1999). These involved selecting a group at random and recording the position of the centre of the group as often as possible while they remained in sight and in the study area. Surface behaviours were recorded for each position using the definitions by Hastie *et al.* (2004). A video camera (Canon Ex2-Hi 8, Surrey, UK) and second observer were used to validate that the same dolphin group was being tracked continually. Any dolphin interactions with
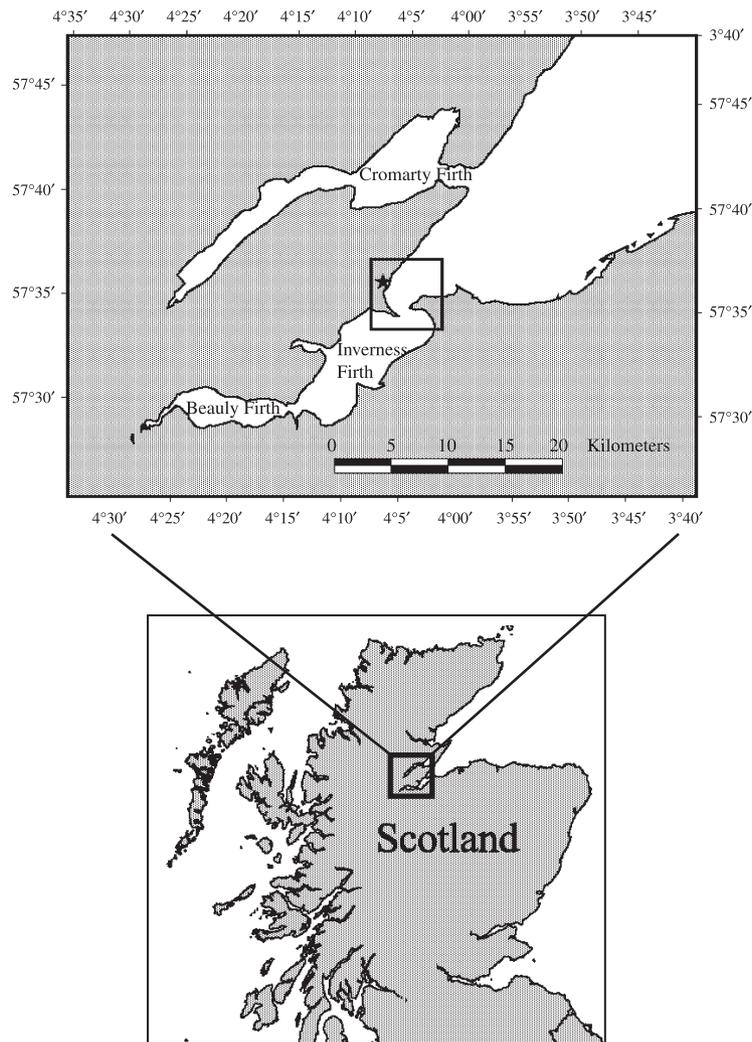
Fig. 1. The location of the study area at the entrance to the Inverness Firth. The observation site is indicated by a black star.

boats, for example bow-riding, were excluded from the analysis because the movements were linked subsequently to the movement of the boat. The longest track from each day, and only those with at least 20 recorded positions, were used in the analysis. Each separate track was considered an independent unit. This assumption was made as photo-identification studies have revealed that the number of individuals frequenting the area is highest during the summer (Wilson *et al.* 1997), the period when this study was conducted. Bottlenose dolphins are also known to live in fission–fusion societies, in which individuals associate in small groups that change in composition, and within this particular population there do not appear to be any sex-specific bonds (Wilson 1995). A large number of different individuals are therefore likely to have been tracked over the survey period. Dolphin position data were stored in ArcView version 3·3 (ESRI, Inc.). Lines connecting sequential points were created using the animal movement extension (Hooge, Eichenlaub & Solomon 1999). Distances and angles were calculated using the path, with distances and bearings extension for ArcView (Jenness 2003).

CRW MODEL

The path characteristic that was used in this model was the net squared displacement and was calculated for the observed movement paths for each sequential move. The net displacement is the straight-line distance from the beginning to the end-point of a path. The displacement is squared, as this tends to grow linearly with time in a CRW (Turchin 1998). Moves were defined as fixed time intervals of 100 s (maximum mean time between consecutive position recordings), interpolated from the raw locations. CRW formulation assumes that move lengths and turning angles are not correlated serially. This was tested by calculating the autocorrelation function (ACF) and the Ljung–Box Q-statistic for all lags up to six moves for move length (Turchin 1998). Angular correlation was determined by defining sequential turns as left or right and performing a runs test to check for non-randomness (Turchin 1998). If the track exhibited significant autocorrelation for either of these parameters, moves were increased to 200-s time intervals and the autocorrelation tests for move length and

turning angle repeated. Visual inspection of the observed net squared displacements indicated that there were tracks that exhibited more than one distinct type of behaviour and were consequently divided into sections. Tracks were grouped based on similarities in observed net squared displacements, mean move lengths and turning angles. Move lengths and turning angles were pooled together within these groups to calculate an average expected net squared displacement and 95% confidence intervals using a bootstrap simulation of 1000 iterations (Turchin 1998). Expected values, $\bar{R}_n^2$ (km), were calculated using the equation by Kareiva & Shigesada (1983) as the turning angles were distributed symmetrically:

$$\bar{R}_n^2 = nl^2 + 2l^2\frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right) \qquad \text{eqn 1}$$

where n is the number of moves from the first location, l is the mean move length (m) and c is the mean of the cosines of the turning angles. Plots of observed and expected values were examined visually to see how each fitted the CRW model. In cases where the observed net squared displacement increased more rapidly than linearly with time, a biased random walk (BRW) model was considered as an alternative. In this model move direction is influenced by the absolute compass direction, whereas in a CRW it is influenced only by the previous move direction. The net squared displacement consequently increases quadratically rather than linearly in a BRW. The expected net squared displacement for a BRW model was calculated by (Marsh & Jones 1988):

$$\bar{R}_n^2 = nl^2 + n(n-1)l^2\theta^2 \qquad \text{eqn 2}$$

where θ is the mean cosine of absolute move direction. The tracks were then assigned a movement type based on whether more than 50% of the moves were within the 95% confidence intervals of the expected values for a CRW, and were therefore described as fitting the model, were under- or overpredicted or mixed between the three states. Alternatively, if more moves were within the 95% confidence intervals of the BRW model, the path was classed as fitting a biased random walk. Fisher's exact test was then conducted to determine whether the proportion of tracks that fit the random walk models or deviated from them differed between those that had moves at 100-s or 200-s time intervals (Zar 1984). General linear model analysis was performed for each of the movement characteristics: mean move length, mean speed, angular concentration (defined as 0 where there is so much dispersion a mean angle cannot be defined and 1 where all data are concentrated in the same direction) and turning angle (defined only as 0–180° for straight-ahead and directly behind, respectively, and irrespective of left- or right-turning direction) to determine if the time interval between moves had a significant effect on the values of these parameters. Differences in these movement characteristics between movement types were examined using a single-factor multiple

analysis of variance (MANOVA). Separate ANOVA analyses were conducted for the two time intervals for the movement characteristics that were found to differ significantly between them. Tukey's *post hoc* tests were performed for those parameters that were affected significantly by movement type to identify the groups that differed. A Rayleigh test was performed for each track to test whether the move angles were distributed uniformly around a circle, having first checked graphically that distributions were not bimodal (Fisher 1993). Nominal logistic regressions were performed to determine if movement type was affected by month or tidal state.

FIRST-PASSAGE TIME MODEL

The FPT is defined as the time required for an animal to cross a circle with a given radius (Johnson *et al.* 1992). Each location point was assigned circles of several radius sizes centred around them. These included a circle radius of 50 m, 100 m and then increasing at 100-m intervals. The first and last parts of the path were excluded as the first-passage times backwards and forwards, respectively, are unknown. The time taken to cross these circles was estimated using the density of points at 44-s intervals along the path as a proxy (the mean time between consecutive positions). This greatly reduced the calculation time, as the number of points within each circle could be determined using the counting point extension (http://software.geocomm.com/scripts/arcview/) in ArcView version 3·3 (ESRI, Inc.). The FPT values were log transformed so that the times were independent of the magnitude of the mean FPT. The circle radius at which the variance in FPT was highest was defined as the spatial scale at which searching effort was concentrated (Fauchald & Tveraa 2003). The longest FPT at this radius size identified the site(s) at which intensive searching was occurring. General linear model analysis was performed to determine whether the size of the search areas and the time allocated to these areas varied with month or tidal state.

A grid was created and overlaid onto the survey area with a cell size equal to the median search diameter for all the tracks. The number of search areas that occurred within each cell of the grid was calculated and the areas with highest overlap were identified as key searching areas.

ASSOCIATION WITH FORAGING BEHAVIOUR

The association between these intensively searched sites and foraging behaviour was investigated by determining the extent to which key surface behaviours associated with foraging occurred inside and outside these searched areas. We defined foraging behavioural events as surfacing with a fish or porpoising (entire body leaves the water and travels more than two body lengths over the surface). The former provided direct evidence of foraging, while porpoising was included because Hastie *et al.* (2004) found that it tended to

co-occur closely with surfacing with a fish. The proportion of location points inside the search areas was then compared with the proportion of points at which these foraging behavioural events had been observed. This was analysed using a Cochran–Mantel–Haenszel test, which tests for independence having adjusted for the random variation between individual tracks (Agresti 2002).

A Spearman's rank correlation was performed to determine whether the number of tracks that had lower than expected net squared displacements coincided with where there was most overlap between the intensive search areas. All statistical analyses were performed using Minitab® 14·1.

Results

A total of 42 surveys were conducted and 26 tracks were used in the analysis. There was a relatively high degree of variability between recorded tracks both in their longevity (mean = 62 min, SD = 35 min) and spatial extent (mean = 5081 m, SD = 3325 m) with an average of 89 recorded locations (SD = 63·82) per track. There was an average of five individuals within a group (SD = 2·3, range = 2–9). The tracks spanned all months of the surveying period. Ten tracks were obtained during 2003 and the remainder in 2004. The majority of tracks were obtained during the flood tide (69%). This is partly as a result of more surveys being conducted on the flood tide (62%). As fewer observations were made closer to the theodolite (within 1 km) than further away, this suggests that sightings were not biased towards detecting animals close to the observation station.

CRW MODEL

Ten tracks had significant autocorrelation in their move lengths or turning angles at a time interval of 100 s. These tracks were analysed at a 200-s interval, at which scale there was no significant autocorrelation. Eight of the tracks were divided into more than one section following visual examination of the observed net squared displacement values resulting in 35 track sections. Nine of the track sections had more than 50% of their moves within the 95% confidence intervals of the expected

net squared displacement and were classed as fitting a CRW model (Fig. 2a). Five track sections had higher than expected displacements. Nine were lower than predicted (Fig. 2b), indicating that these animals remained closer to their initial location than expected. Four tracks had moves spanning these three categories almost equally, indicating a mixture of movement behaviours. Eight tracks fitted a BRW model more closely (Fig. 2c). In four of these tracks the mean move direction was 5–27° and in three tracks 186–196°, approximately reciprocal bearings. The remaining track had a mean move direction of 150°.

There was no significant difference in the proportion of track sections that fitted or deviated from a random walk model for the two time intervals (Fisher's exact test: $P = 0·47$). General linear model analysis revealed that only move length differed significantly between the two time intervals, with move lengths being significantly longer for the higher time interval as expected ($F = 4·59$, d.f. = 1, 29, $P = 0·041$). There was no significant effect of movement type on move length for either time interval (ANOVA for 100-s and 200-s intervals, respectively: $F = 2·34$ and 1·44, d.f. = 3, 19 and 2, 6, $P = 0·106$ and 0·308). The remaining movement characteristics were analysed using a MANOVA. No transformations were applied to the parameters as the assumptions were upheld. There was no significant difference in mean speed with movement type, but there was in angular concentration and turning angle (MANOVA Pillai's test statistic: $F = 2·57$, d.f. = 12, 90, $P = 0·006$). Tukey's *post hoc* tests showed that the angular concentration was significantly higher for those track sections fitting a BRW model than those that were under- or overpredicted by a CRW model or a mixture of these behaviours (Table 1). Turning angle was significantly lower for track sections fitting a BRW than for those overpredicted by a CRW model or a mixture of movement behaviours (Table 1). The Rayleigh tests were significant for all the track sections except for two, indicating that successive moves showed a mean direction and a CRW model was therefore appropriate to use instead of a pure random walk model. There was no significant effect of tidal state or month on movement type (nominal logistic regression: $G = 4·109$ and 5·351, d.f. = 4 and 4, $P = 0·392$ and 0·253, respectively).

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Table 1. Mean movement characteristics ± SE by movement type. The parameter move length is separated into 100-s and 200-s time intervals, and no SE is given when there is only a single track section for that movement type. Significant differences are based on Tukey's *post hoc* tests. [B] indicates significantly different from BRW and [C] significantly different from CRW movement type

| Movement characteristic	BRW	CRW	Underpredicted by CRW	Overpredicted by CRW	Mixture of types
Move length (m)					
100 s	172·1 ± 21·4	127·3 ± 18·1	139·8 ± 26·4	86·3 ± 26·0	133·9
200 s	238·2 ± 25·6	144·5	215·2	147·6 ± 70·0	130·7 ± 37·6
Speed (m s^{-1})	1·52 ± 0·17	1·18 ± 0·19	1·33 ± 0·21	0·82 ± 0·20	0·81 ± 0·22
Angular concentration	0·88 ± 0·04	0·80 ± 0·06	0·61 ± 0·04[B]	0·64 ± 0·03[B]	0·57 ± 0·08[B,C]
Turning angle (°)	27·72 ± 5·81	46·01 ± 7·37	56·41 ± 7·26	63·77 ± 8·14[B]	90·2 ± 24·4[B,C]

(a)

(b)

(c)
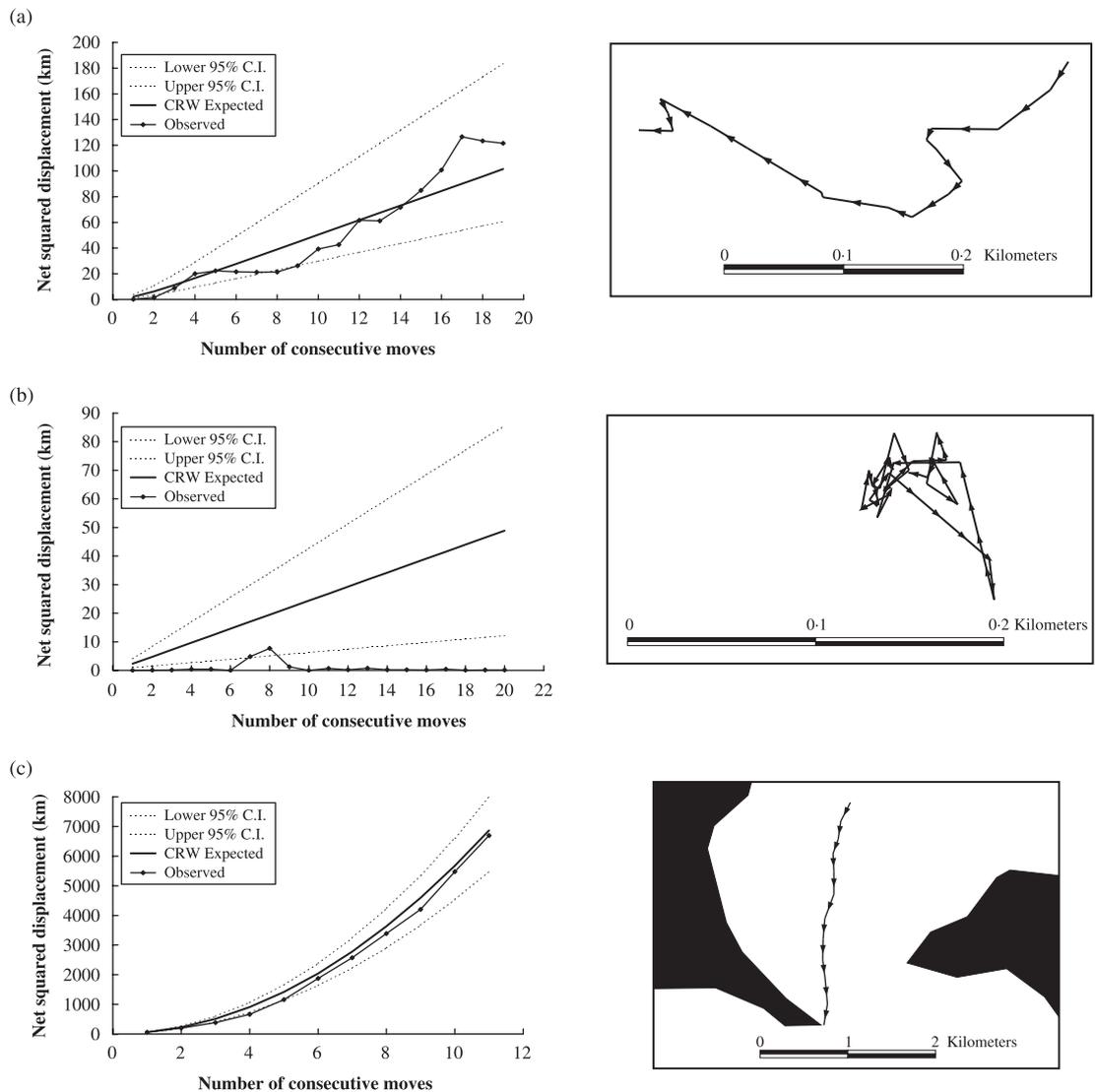
Fig. 2. Three examples of observed and expected net squared displacements with their corresponding tracks (arrows indicate the direction of movement). (a) Observed displacement fits a correlated random walk model. (b) The observed displacement is lower than expected. (c) The observed displacement fits a biased random walk model.

FIRST-PASSAGE TIME MODEL

An example of the assignment of searched areas to the tracks is given in Fig. 3. Half the tracks had a search radius of 50 m and the majority (88%) had intensive search areas that were less than 300 m in radius. There were two tracks with larger radii at 600 and 700 m. Dolphins remained within their search areas for a mean duration of 22 min (SD = 27·74 min), but in one track dolphins remained within their search area for over 2 h. There was no significant effect of month or tidal state on the spatial scale of the intensively searched area (general linear model: $F = 0.50$ and 0.41, d.f. = 3, 3, 19, $P = 0.688$ and 0.751, respectively) or on the time allocated to these areas (general linear model: $F = 0.58$ and 0.69, d.f. = 3, 3, 19, $P = 0.638$ and 0.569, respectively). The median search radius was 100 m, so a 200 × 200 m grid cell was used to investigate the degree of overlap between search areas. The area used most repeatedly

was off the peninsula Chanonry Point. The low relief of the beach in this area meant that observations could also be made beyond the peninsula from the theodolite station. Overlap also occurred off the opposite peninsula and in the centre of the main channel (Fig. 4a).

The tracks in the lower quartile of maximum variance in first passage time ($n = 6$) indicated those that spread their time most evenly along the pathway. Two of these tracks appeared to move through the study area in a relatively straight line, indicating that the site was being used as a passageway. One track headed towards Chanonry in a relatively straight line, but then returned outwards. The remaining three tracks were recorded over only small areas of about 1 km², so it is unknown whether the animals continued to pass through the channel. However, the pathways were recorded for 25–56 min and the dolphins were moving at an overall mean speed of 1·15 ms⁻¹ (SD = 0·57 ms⁻¹), which should result in them travelling 1 km in approximately 17 min.
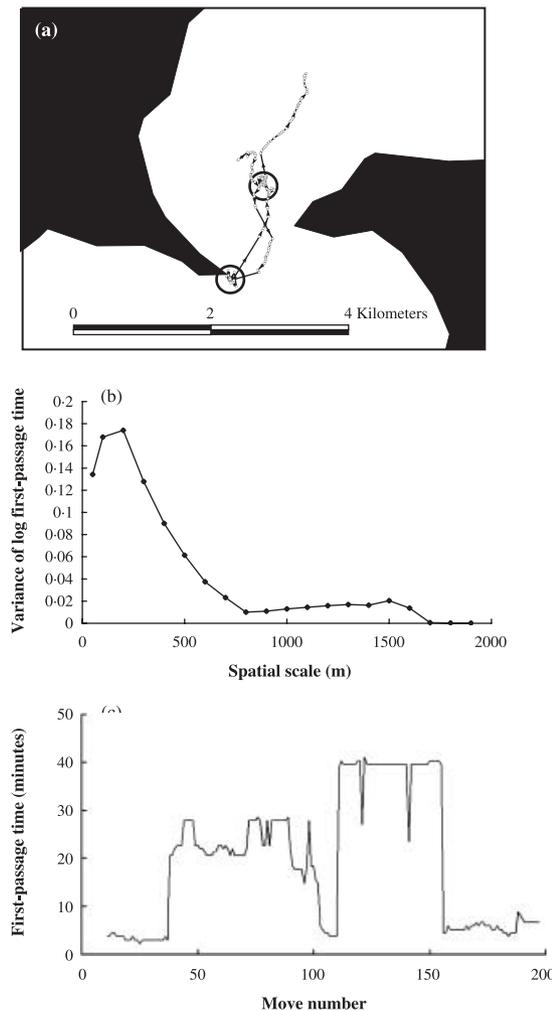
Fig. 3. An example track with (a) recorded dolphin group positions given as the small circles and the large circles represent the 200 m radius intensive search areas; (b) the variance in first-passage time for circles of different radius peaking at 200 m radius; and (c) first-passage time for each move across a 200 m radius circle.

This suggests that travelling through the area was unlikely to be their sole activity during this period.

ASSOCIATION WITH FORAGING BEHAVIOUR

Fish tossing and porpoising were observed during 12 of the tracks and on 21 occasions. These foraging behaviours were significantly more likely to occur inside an intensively searched area (Cochran–Mantel–Haenszel statistic = 8·5563, d.f. = 1, $P = 0·003$) (Fig. 4b). There was a significant positive relationship between the number of tracks that had lower than expected net squared displacements and the number of intensive search areas within the 200×200-m grid cells (Spearman's rank correlation: $r = 0·343$, $P < 0·001$).

Discussion

Modelling movement as a CRW provides a firm foundation from which to investigate the foraging strategies
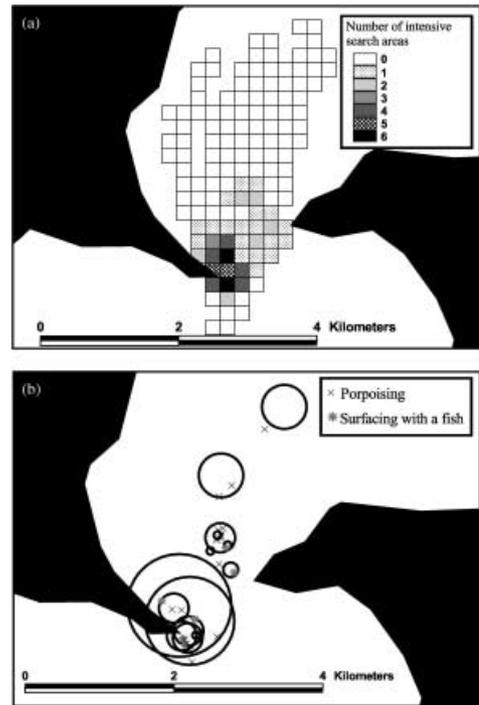
Fig. 4. (a) Overlap between the intensive search areas within 200×200 m grid cells is indicated by the degree of shading. The extent of the grid gives the range over which dolphin positions were recorded. (b) Locations of foraging behaviour, defined as surfacing with a fish and porpoising, and intensive search areas for those tracks in which these behaviours were observed.

of animals and develop more complex models. This has rarely been used to quantify the movement of large animals and generally at only coarse spatial and temporal scales. The FPT approach allowed quantification of the time allocation to patches and enabled both the identification of the spatial scale and location of areas where search effort was concentrated (Fauchald & Tveraa 2003).

Only a quarter of the track sections were classed as CRW movement, despite the key assumptions of no serial correlation in move lengths or turning angles being satisfied. In contrast to the CRW model, in which directionality is determined internally based on the previous move direction, a BRW is characterized by external directionality as a fixed compass direction is followed. This suggests that the dolphins are capable of using cues based not only on their recent prior experience to find suitable foraging areas, but over a larger temporal and spatial scale. It may also indicate a preference for particular habitat characteristics to aid them in finding food, as the dominant compass direction followed the main northern deep channel through the study area.

BRW movement was characterized by significantly smaller turning angles than those trajectories moving very short net distances (overpredicted by the CRW model). Turning behaviour is therefore an important factor determining whether movement is strongly directional or concentrated within a small area. The identification of distinct behaviour types, which may

occur within the same track, reveals that the animals switch between different types of movement on relatively fine-scales. Such switches in behaviour have also been demonstrated in several other species (Morales & Ellner 2002; Jonsen, Flemming & Myers 2005). Morales *et al.* (2004) found that to describe elk movement, models with two movement states usually outperformed the single model. Although two distinct movement types were identified in our study, a high degree of variability in the movement parameters, turning angle and move length, between tracks may reflect responses to local environmental conditions (Kareiva & Shigesada 1983; Jonsen & Taylor 2000) or individual variability (Pinaud & Weimerskirch 2005).

The presence of two distinct modes of behaviour provides evidence that the dolphins were displaying area-restricted search behaviours. When prey are present in clumps, this tactic can achieve a higher energy gain than using only one mode or moving randomly (Nolet & Mooij 2002). These behaviours may therefore be in response to the patchy distribution of prey, as has been demonstrated in copepods (Tiselius 1992). In plaice, intensive search behaviour was characterized by short movements and frequent turning (Hill, Burrows & Hughes 2000). Tuna displayed both an increase in turning rate and lower swimming speeds (Newlands, Lutcavage & Pitcher 2004).

The FPT approach revealed that animals varied the amount of time they allocated to different areas along their movement paths. Although the study area encompasses the only route to more inshore parts of the Moray Firth, the movement patterns recorded in this study indicate that it does not act solely as a passageway. On the majority of occasions, dolphins spent large amounts of time in small, localized areas within the channel. Furthermore, they often did not continue on to the higher reaches of the Firth, but returned outwards. This suggests that the entrance to the Inverness Firth is a site selected specifically by the dolphins and is not simply acting as a bottleneck. The sites of concentrated search effort appeared to be foraging locations and may explain the dolphins' preference for this area.

Search activity was confined generally to relatively small areas (< 300 m radius). Pienkowski (1983) found that plovers moved less far after taking large prey than after taking small or no prey. This suggests that the small search radii could be a consequence of large, highly nutritional prey being taken in this area. Alternatively, it may reflect the size of the prey patches. Nolet & Mooij (2002) found that there was a match between the scale of food clumps (pondweed tubers) and the movement patterns of swans, indicating that they were causally linked. The scale and location could also be representative of the areas in which prey could be caught. There may be specific habitat characteristics or fish school sizes that enable prey to be caught more easily by the dolphins. Studies on killer whales have found that they feed on small schools of herring in an area where herring is mainly present in large shoals (Similä 1997). It is possible that smaller groups make it easier for the predator to target individual prey.

Overlap in search effort was highest in three key areas. The area off one of the peninsulas, Chanonry Point, was used the most frequently. It also tended to have the longest search durations and hence time allocation, indicating that foraging success was greatest in this area. The other frequently searched sites were off the peninsula on the other side of the channel and in the centre of the main channel. These three sites all have steep seabed slopes and rapidly reach depths of over 40 m. The water current speed around the peninsulas and in the centre of the deep-water channel is also considerable, and may reach 3·5 knots during the spring tide (Admiralty Chart 1077). High frequencies of cetacean sightings off headlands and narrow channels have also been observed in other areas (Ingram & Rogan 2002; Simard, Lavoie & Saucier 2002). These features may aid the capture of fish by increasing their ability to detect or manipulate prey and provide barriers against which to herd them (Hastie *et al.* 2004).

Predators may be attracted to predictable aggregations of prey rather than to areas with the highest prey densities, as they have incomplete knowledge of prey distributions (Begg & Reid 1997). Hydrographic processes can result in features that provide such predictable aggregations of prey. Associations between fronts and seabirds (Decker & Hunt 1996; Skov & Prins 2001) and marine mammals (Brown & Winn 1989; Tynan 1997; Mendes *et al.* 2002) have been observed, suggesting a preference for predictable food sources by these animals. A tidal front forms in the area at the centre of the main channel (Helen Bailey unpublished data) where overlap of search effort was high, indicating that the dolphins regularly foraged there. The results from this study can be examined in relation to environmental factors such as these. In the marine environment, water currents can have a significant effect on the direction and speed of movement over ground and their impact could also be further investigated using these techniques.

This study has provided insight into the fine-scale movement patterns of bottlenose dolphins and demonstrated the use of two quantitative techniques to further our understanding of their foraging strategies. Evidence of both extensive and intensive search behaviours are likely to be in response to the patchy distribution of prey, and indicates that this spatial autocorrelation can be used by marine predators to find food. These movement patterns can therefore be used to determine the function of different habitats and identify sensitive areas. The techniques have the potential to be applied to a wide variety of species, particularly as the accuracy of tracking technology continues to increase (Ryan *et al.* 2004), and are valuable analysis tools where prolonged visual observation of the subject is not feasible.

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