

Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics

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Summary

1. Search processes play an important role in physical, chemical and biological systems. In animal foraging, the search strategy predators should use to search optimally for prey is an enduring question. Some models demonstrate that when prey is sparsely distributed, an optimal search pattern is a specialised random walk known as a Lévy flight, whereas when prey is abundant, simple Brownian motion is sufficiently efficient. These predictions form part of what has been termed the Lévy flight foraging hypothesis (LFF) which states that as Lévy flights optimise random searches, movements approximated by optimal Lévy flights may have naturally evolved in organisms to enhance encounters with targets (e.g. prey) when knowledge of their locations is incomplete.

2. Whether free-ranging predators exhibit the movement patterns predicted in the LFF hypothesis in response to known prey types and distributions, however, has not been determined. We tested this using vertical and horizontal movement data from electronic tagging of an apex predator, the great white shark *Carcharodon carcharias*, across widely differing habitats reflecting different prey types.

3. Individual white sharks exhibited movement patterns that predicted well the prey types expected under the LFF hypothesis. Shark movements were best approximated by Brownian motion when hunting near abundant, predictable sources of prey (e.g. seal colonies, fish aggregations), whereas movements approximating truncated Lévy flights were present when searching for sparsely distributed or potentially difficult-to-detect prey in oceanic or shelf environments, respectively.

4. That movement patterns approximated by truncated Lévy flights and Brownian behaviour were present in the predicted prey fields indicates search strategies adopted by white sharks appear to be the most efficient ones for encountering prey in the habitats where such patterns are observed. This suggests that *C. carcharias* appears capable of exhibiting search patterns that are approximated as optimal in response to encountered changes in prey type and abundance, and across diverse marine habitats, from the surf zone to the deep ocean.

5. Our results provide some support for the LFF hypothesis. However, it is possible that the observed Lévy patterns of white sharks may not arise from an adaptive behaviour but could be an emergent property arising from simple, straight-line movements between complex (e.g. fractal) distributions of prey. Experimental studies are needed in vertebrates to test for the presence of Lévy behaviour patterns in the absence of complex prey distributions.

Key-words: Lévy walk, migration, optimal foraging, random walk, search behaviour, strategy, superdiffusion, telemetry, archival tracking

Introduction

A general problem relevant to physical, chemical and biological systems is what search strategy should a searcher employ

to find target sites when it possesses incomplete information of the target locations (Shlesinger 2009). In ecology, recent progress in optimal foraging theory has drawn much from concepts and methods used in statistical physics to quantify diffusion processes (Bartumeus & Catalan 2009). One class of stochastic process that has received particular attention in this context is the Lévy flight (Viswanathan *et al.* 2011). Lévy

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flights are a special class of random walk having movement displacements (steps) drawn from a probability distribution with a power-law tail (the so-called Pareto-Lévy distribution) (Shlesinger & Klafter 1986). Lévy flights describe a movement pattern composed of many small steps connected by longer relocations, with this pattern repeated across all scales, such that $P(l_j) \sim l_j^{-\mu}$, with $1 < \mu \leq 3$, where l_j is the flight length (move-step length) and μ the power-law exponent. Because Lévy flights comprise instantaneous flight lengths, hence involve infinite velocities, only the Lévy walk (Shlesinger & Klafter 1986) is biologically plausible because it considers a finite velocity walk with displacement determined after a time t , thus reflecting a dynamical process such as movement (Shlesinger, Zaslavsky & Klafter 1993).

Theory demonstrates that Lévy flights and walks are a more efficient search strategy than Brownian motion for locating randomly distributed targets (Shlesinger & Klafter 1986; Shlesinger 2009). Furthermore, Lévy search model simulations show an optimal exponent of $\mu \approx 2$ for the power-law move-step frequency distribution, when target sites are sparsely and randomly distributed and can be revisited any number of times (Viswanathan *et al.* 1999; Bartumeus *et al.* 2002). In contrast, theoretically, the best movement strategy to adopt when targets are non-revisitable – i.e. when they are completely consumed or disappear – is a ballistic Lévy random walk ($\mu \rightarrow 1$) (Santos *et al.* 2004). Thus, the Lévy flight foraging (LFF) hypothesis proposes that because Lévy flights can optimise random searches of individual foragers, organisms should have naturally evolved to exploit movements that are approximated by Lévy flights (Viswanathan *et al.* 2011). There is burgeoning empirical evidence that diverse organisms display movements approximated by Lévy flights, including insects (Cole 1995; Maye *et al.* 2007; Reynolds *et al.* 2007), reptiles, fishes and aquatic birds (Sims *et al.* 2008; Humphries *et al.* 2010) and frugivorous monkeys (Ramos-Fernández *et al.* 2004). Based on the empirical and simulation results, it has been argued that Lévy flight search is an adaptive behaviour rather than an emergent property of prey distributions (Maye *et al.* 2007; Sims *et al.* 2008). More recently, it was demonstrated (Humphries *et al.* 2010) that animals do not undertake movements approximated by Lévy flights at all times and in all types of environments, but that other behaviour patterns intersperse the movement time series. This tendency presents an opportunity to test the predictions of the LFF hypothesis by determining whether foragers undertake the theoretically optimal movement patterns appropriate to the environments which they occupy and which necessarily have different resource conditions (prey types, abundances and distributions).

Two predictions arising from the LFF hypothesis are that Lévy flight movements should occur more frequently in environments with sparse prey, whereas Brownian-type motion should occur where prey is abundant (for review see Viswanathan *et al.* 2011). A recent natural experiment to test these predictions mapped movements of electronically tagged large marine fishes in environments with different general levels of primary productivity and analysed time series of vertical dis-

placements in each environment type (Humphries *et al.* 2010). The results of the latter study supported the broad predictions of the LFF hypothesis, lending some support to the contention that organisms naturally evolved optimal Lévy flight movements to exploit resource-sparse environments. However, one limitation of the study (Humphries *et al.* 2010) was that satellite remote-sensing images of chlorophyll 'a' concentration in phytoplankton were used as a proxy for primary productivity, and consequently, as an indirect measure of resource abundance and distribution in each environment. This is a reasonable approach given the general lack of broad-scale maps with sufficient spatial resolutions of prey density, such as fishes and squid (Sims *et al.* 2006; Tittensor *et al.* 2010), with which to test the hypothesis on marine predators. Nevertheless, given that marine predators such as large fish do not feed directly upon phytoplankton, it remains to be tested whether Lévy or Brownian movements of free-ranging predators actually reflect prey characteristics. If there was evidence in support of predators exhibiting movement patterns expected theoretically for the types of prey fields encountered, it would provide some support for the idea that animals may acquire stochastic processes to optimise behaviour (Maye *et al.* 2007; Bartumeus 2009).

We tested this using movement data of electronically tagged great white sharks *Carcharodon carcharias*, off Australia and with respect to known locations and types of its prey. The white shark is a coastal and offshore inhabitant of continental and insular shelves and oceanic islands circum-globally, reaching at least 6 m total length and actively hunting a broad range of prey, from small bony fishes and elasmobranchs to marine mammals such as seals, sealions, dolphins and whale carrion. Two of us (DWS and NEH) analysed the time series of vertical displacements of white sharks to identify the presence of Lévy and Brownian signals and to determine when these sequences occurred during each track (see Materials and methods; Humphries *et al.* 2010). Horizontal tracks were not suitable for this analysis because of occasional long gaps between locations in the time series (Bradshaw, Sims & Hays 2007). Therefore, from vertical movement analysis results alone we made predictions about the likely prey category or relative prey abundance the sharks may have encountered (Table 1). We set out the following predictions: (i) sparsely distributed prey in revisitable patches were present when optimal Lévy (power-law distributed) movements occurred where $\mu \approx 2$. Revisitable patches were defined as prey aggregations that are not entirely depleted by a predator and subsequently reform into a patch or school (e.g. in the pelagic zone where widespread physical habitat to facilitate hiding is not available); (ii) sparsely distributed prey in non-revisitable patches were present when optimal Lévy (power-law distributed) movements occurred where $\mu \rightarrow 1$. Non-revisitable patches were classed as those where the prey is consumed entirely or disperses/hides and does not reform aggregations over times when the predator is present (e.g. in areas where habitats are physically complex and facilitate escape or hiding behaviours) (Viswanathan *et al.* 2011); and (iii) abundant prey were present either when Brownian

Table 1. Summary of prey characteristics predicted from quantitative movement analysis with those known to occur in habitats visited by tagged white sharks. Comparison shows good agreement of results with the Lévy flight foraging hypothesis

Shark	Time-series section	Best-fit model (P, power law; T, truncated power law; E, exponential)	μ value (P and T models only)	Predicted prey characteristics (from model)	Known prey characteristics in habitat occupied by shark	Model consistent with prey fields (Yes/No)
1	1	P	2.55	Sparse, revisitable targets	Open shelf or oceanic prey	Y
	3	T	1.76	Sparse, revisitable targets	Open shelf or oceanic prey	Y
	4	T	1.77	Sparse, revisitable targets	Open shelf or oceanic prey	Y
2	1	E		Abundant targets	Seal colony	Y
	2	T	1.32	Sparse, non-revisitable	Fast-moving/less detectable fish; turbid habitat	Y
	3	T	1.11	Sparse, non-revisitable	Fast-moving/less detectable fish; turbid habitat	Y
3	4	T	1.11	Sparse, non-revisitable	Fast-moving/less detectable fish; turbid habitat	Y
	1	T	2.27	Sparse, revisitable targets	Fish aggregations; coastal and open shelf	N
	2	T	2.01	Sparse, revisitable targets	Open shelf or oceanic prey	Y
4	3	E, T		Abundant/sparse targets; ambiguous support	Fish aggregations; coastal and open shelf	–
	2	E		Abundant targets	Fish aggregations; coastal	Y
	3	E, T		Abundant/sparse targets; ambiguous support	Fish aggregations; coastal and open shelf	–
	4	E		Abundant targets	Fish aggregations; coastal	Y

Sections for sharks 1 (section 2) and 4 (section 1) were not included in the analysis as the best model fits were to data ranges < 1.2 decades. '–' in last column denotes that no clear prediction was possible, but where two or more predictions may be relevant to explain behaviour patterns at finer spatiotemporal scales of movement.

(exponentially distributed) movements occurred or where the Lévy exponent $\mu > 3$. A prediction about the prey category was assigned to each movement time-series section and specifically tested by mapping vertical movements onto the horizontal tracks reconstructed from tagging data by field researchers (BDB, RWB), including information on the different prey types present and generally taken by white sharks occupying those habitats.

Materials and methods

STUDY ANIMALS AND TAGGING

White sharks were fitted with four different electronic tags as part of discrete studies into their broad-scale movement patterns and habitat use in Australian waters. Tags (see details below and in Table S1, Supporting information) were either placed on free-swimming white sharks using a stainless steel dart with a 316 stainless steel-braided wire leader inserted into the dorsal musculature near to the base of the first dorsal fin using a tagging pole (pop-off satellite-linked archival tags, (PSAT) or a data-logging archival tag, DAT; Wildlife Computers, USA), or sharks were captured, temporarily restrained in an in-water stretcher and a data-logging Argos satellite tag (SPLASH; Wildlife Computers, Seattle, WA, USA) attached to the first dorsal fin using stainless steel bolts. Acoustic tags were surgically implanted into the body cavity via a small incision anterior to the cloaca. Full details of the tagging procedures used are given elsewhere (Bruce, Stevens & Malcolm 2006; Bruce & Bradford 2011). Sharks 1 and 2 were fitted with PSAT and DAT devices, respectively, shark 3 with PSAT, SPLASH and acoustic tags, and shark 4 with PSAT and acoustic tags. Analyses were made using the full archival records of vertical movements of three returned PSATs and one DAT, and horizontal movements were mapped using data from PSAT, SPLASH and acoustic tags.

TIME-SERIES DIVISION

Long and complex dive time series (vertical tracks) recorded by animal-attached electronic tags probably capture a series of different movement behaviours. Rather than analysing an entire time series, we divided each track into sections to help identify clearer patterns. We applied a split-moving window (SMW) analysis similar to that described by Cornelius & Reynolds (1991) to all four white shark tracks. Our method is described in detail elsewhere (Humphries *et al.* 2010). Briefly, we constructed a two-dimensional time-at-depth matrix, with 6-h time bins (as columns) and 10-m-deep bins (as rows), from the raw dive time-series data by calculating the proportion of time spent at each depth within each time period. A virtual window with a width of six time bins was placed at the start of the time-at-depth matrix, and a measure of dissimilarity (Euclidean distance between averaged time at each depth) between the two window halves was calculated and assigned to the centre position of the window. Window position was then advanced by one time bin and the calculation repeated until the end of the time series. Statistical significance of each dissimilarity value was calculated using a Monte Carlo technique whereby the calculation is repeated 1000 times with a shuffled time-at-depth matrix. The number of times the dissimilarity value exceeds that calculated using the real data is counted and converted to a percentage that represents the *P*-value. Significant discontinuities in the time series will have higher dissimilarity values than most of those calculated using a random rearrangement of the data, resulting in very few randomisations yielding higher dissimilarity values. The width of the window was then incremented by two and the process repeated up to a width of 32, giving 14 window sizes. The *P*-values calculated from each window size and position are plotted by stacking them vertically, with significant values (in this case $P < 0.001$) being plotted in black (e.g. Fig. 1). Discontinuities in the dive time series are revealed by the presence of inverted triangles which 'point' to the discontinuity and indicate the position at which the time series can

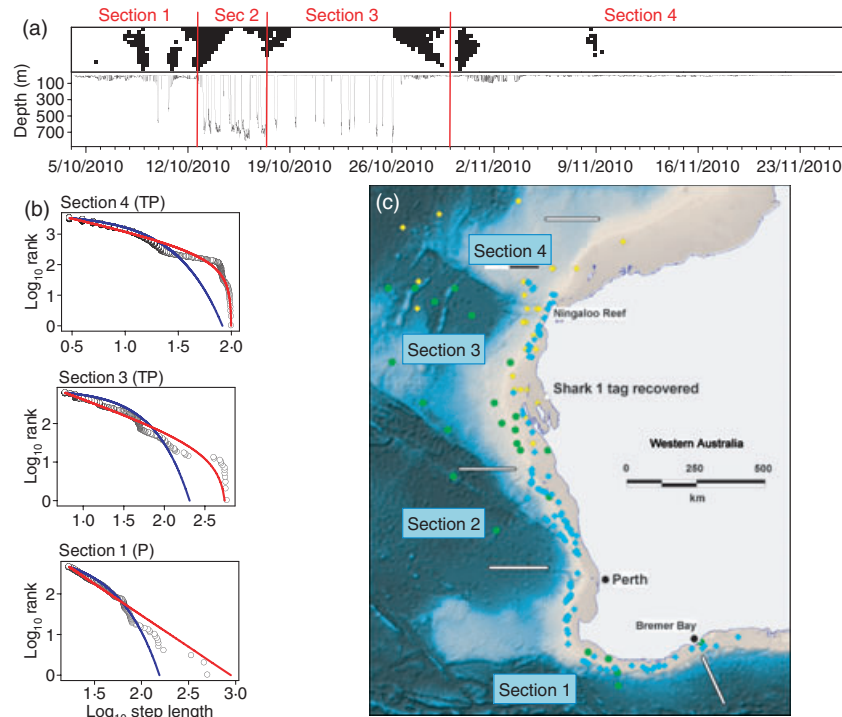


Fig. 1. Evidence for power-law scaling of diving movements of a white shark (no. 1) during long-distance travel through prey-sparse environments. (a) Time series of vertical dive displacements separated into sections using split-moving window analysis (upper panel), where black triangles 'point' to transitions (see Materials and methods). (b) Rank-step-length frequency plots (black circles are observations) for sections 1, 3 and 4 showing power-law and truncated power-law best fits (red lines) compared with exponential fits (blue). Best model fit for section shown in parentheses after section number; TP, truncated Pareto; E, exponential. Section 2 not shown, data range was < 1.2 decades. (c) Map showing the reconstructed track of shark 1 off Western Australia as it moved from Bremer Bay to Ningaloo Reef. Sections 1–4 correspond to the dive sections in (a) and (b). Tagged shark geolocations are shown, as estimated from tag-recorded changes in light intensity (yellow diamonds) and sea surface temperature (green circles). Blue diamonds show Argos satellite-transmitter locations for a different white shark tagged near the North Neptune Islands to illustrate the route often taken by white sharks up the west coast of Australia, and which is consistent with the route of shark 1. White triangle denotes tag retrieval location. Bathymetry: brown colours denote continental shelf < 200 m depth; light blue denotes depths > 200 m, dark blue > 1000 m.

be divided as a quantitative estimate of where different movement patterns are located in the time series.

DATA ANALYSIS

Prior to performing maximum likelihood estimation (MLE) analysis, all sections, which comprised time-stamped depth measurements, were converted into move-step lengths by calculating vertical movement deltas between successive pairs of data points. Steps that were part of a single movement (i.e. where the trend of consecutive steps was either a continuously increasing or decreasing depth) were coalesced into a single step rather than many smaller steps. It should be noted that this method of path integration maintains move-step lengths consistent with that of a Lévy walk because displacements have finite velocity and are dependent on a time t . The MLE methodology employed was described by Clauset, Shalizi & Newman (2009) with power-law, truncated Pareto-Lévy (truncated power law) and exponential distributions tested. Detailed methods and the equations used to estimate the exponent in the MLE analysis and to generate best-fit data sets are given elsewhere (Humphries *et al.* 2010). The approach to best-fit model selection in this study was to use MLE, log-likelihoods (LL) and Akaike Information Criteria (AIC) weights (w AIC) in addition to visual inspection for assessing best fits to rank-step length plots of observed data. Once MLE best-fit parameters for

the three candidate distributions [power law, truncated Pareto (power law) and exponential] had been derived, the observed data and best fits were plotted as log₁₀ rank vs. log₁₀ step length and were assessed visually to determine which, if any, of the three candidate distributions provided a reasonable fit. Log-likelihoods were calculated (Burnham & Anderson 2004) for the two competing models for each section, and w AIC were used to select the best-fit model to test the LFF hypothesis.

Results

ANALYSIS OF VERTICAL DISPLACEMENTS

The time series of swimming depths for four white sharks totalling 1 239 957 data points were separated into more behaviourally consistent sections for potentially clearer signal identification using a split-moving window analysis (see Electronic Data S1; Tables 1 and S2, Supporting information). The time series of shark 1 was separated into four sections (Fig. 1). Maximum likelihood best-fit models to rank-step length plots (see Materials and methods) for all sections, where the move-step length data range spanned > 1.2 orders of magnitude (i.e. sections 1, 3 and 4), were found to

be power law (Lévy) or truncated power law (truncated Lévy) distributed. For sections 1, 3 and 4, the μ exponents were 2.55, 1.76 and 1.77, respectively. The prediction for this track was that during sections 3 and 4, movements were consistent with searches for sparsely distributed prey forming patches that can be revisited (prediction 1). Although section 1 was also consistent with this expectation, the μ exponent was > 2.5 , indicating that fewer longer steps were undertaken and that part of the track may have included movements approximated by an exponential distribution because $\mu > 3$ emerges as Brownian motion.

The time series of shark 2 was also separated into four sections. The pattern of vertical movements in section 1 was best fit by an exponential distribution, while the remaining sections were best fit by truncated power-law distributions with low μ values within the Lévy range of between 1.10 and 1.32 (Fig. 2). The model fit to data in section 1 predicts movements consistent with Brownian motion where prey is abundant (prediction 3). However, truncated Lévy flight model fits to sections 2–4 with exponents approaching 1, characterising ballistic motion, indicate optimal search for sparse prey where patches are non-revisitable (prediction 2).

The time series of shark 3 was split into three sections. Sections 1 and 2 provided model best fits to a truncated power-law distribution with $\mu = 2.27$ and 2.01, respectively

(Fig. 3), consistent with an optimal search for sparsely distributed resources (prediction 1). Section 3 was equivocal, with both truncated Lévy and exponential best-fit models receiving good support (Akaike weights) over the respective data ranges selected (Table S2; see Materials and methods), perhaps indicating a mixed pattern of movement, between Brownian and Lévy behaviour. Lastly, the time series for shark 4 was separated into four sections; section 1 was excluded from analysis as fits were only obtained over a data range of 0.5 orders of magnitude. Sections 2 and 4 yielded best fits to an exponential model, predicting abundant prey fields (prediction 3). However, for section 2, the heavy tail of the distribution was not entirely well fitted by this model; visually, the truncated Lévy distribution provided a better fit to the extreme tail (Fig. S1, Supporting information). Section 3 yielded good model support for both Lévy and exponential models over the respective data sets chosen, suggesting potentially complex behaviour, as found for shark 3 (section 3).

HORIZONTAL MOVEMENT AND PREY FIELDS

Overall, there were 15 sections of vertical move-step data for mapping analysis. We made 11 clear predictions (Table 1) with a further 4 sections unable to support one prediction because either model fit data ranges were < 1.2 decades (2

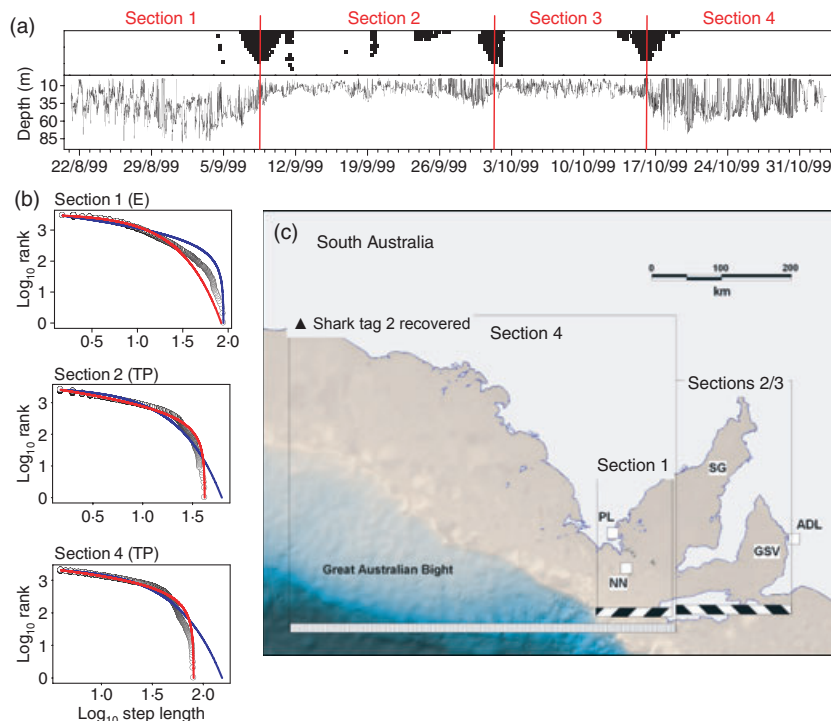


Fig. 2. Evidence for Brownian movements of white shark 2 near an abundant food source prior to switching to truncated power-law distributed movements in adjacent areas where prey is less predictable. (a and b) As for Fig. 1, except section 3 rank-frequency plot not shown since similar to that of section 2 from the same geographical area. (c) Map showing the estimated changes in area occupancy of shark 2 off South Australia corresponding to the different sections of dive patterns in (a). The shark was tagged at the North Neptunes (NN) seal colony and was captured in a fishing net in the Great Australian Bight (white triangle). Area occupancy of shark 2 was determined using light-level geolocation (for review see Makris *et al.* 2006) and areas were published previously in Martin *et al.* (2005). PL, Port Lincoln; SG, Spencer Gulf; ADL, Adelaide; GSV, Gulf St Vincent. Bathymetry: see Fig. 1 legend.

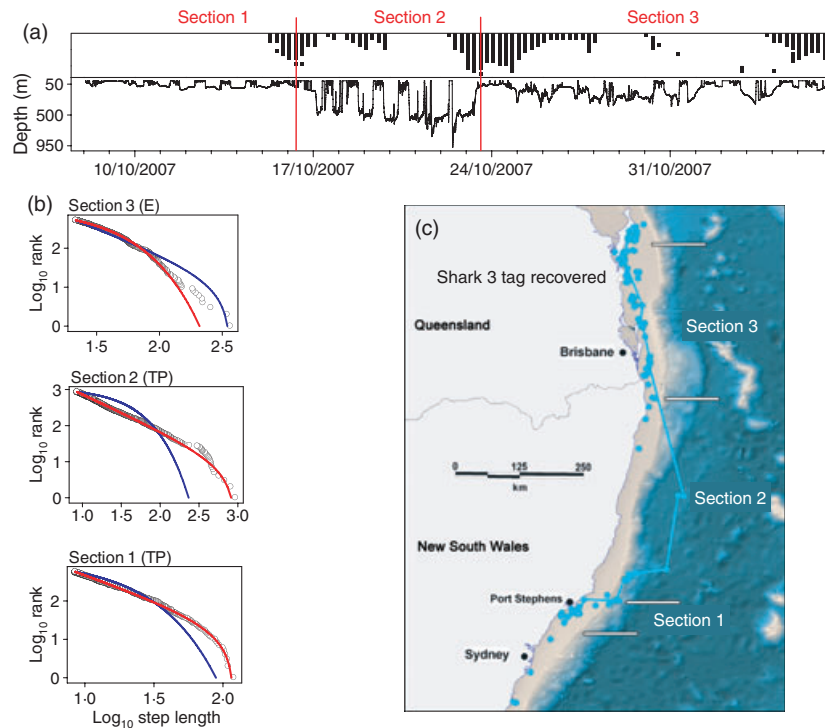


Fig. 3. Evidence for truncated power-law distributed diving movements of white shark 3 in open ocean habitats with sparse prey. (a and b) As for Fig. 1. (c) Map showing the Argos satellite-tracked movement of shark 3. Positions joined by lines indicate the period prior to pop-off satellite-linked archival transmitter tag release where the sharks were heading northwards along the east coast of Australia. Bathymetry: see Fig. 1 legend.

sections), or equal support for truncated power-law and exponential models was found (2 sections; Table S2). Of the 11 sections where predictions were made, 10 were consistent with the LFF hypothesis (Table 1).

Shark 1 was tagged with a PSAT while freely swimming off Bremer Bay in southern Western Australia (Table S1). Light-level and sea surface temperature-based geolocation estimations (reviewed in Sims 2010) indicate that the shark moved west and then northward towards the Ningaloo Reef region of north-west Western Australia. The tag was physically recovered from Shark Bay after it popped up just to the west of this location (Fig. 1). White sharks travel on average at 3.5 km h^{-1} in Australian waters (Bruce, Stevens & Malcolm 2006) so assuming this rate of travel, and from the estimated light-level/SST-based geolocations, the white lines in Fig. 1 approximate the location of section breaks in the vertical displacement time series. Section 1, therefore, represents open shelf movements close to the shelf edge in south-west Western Australia. The shark was tagged in the vicinity of a seal colony, an abundant stable food source, remaining there only a short time before travelling west consistently afterwards. This could account for the higher exponent of the truncated power law (> 2.5) found in section 1, with movements being influenced to some degree by abundant prey at the start of the track (prediction 3). For the remainder of the tracking, shark 1 travelled in a directed manner heading consistently north and completing the *c.* 2000-km journey in *c.* 24 days (averaging the expected 3.5 km h^{-1}). While travel-

ling, it moved vertically with patterns approximating optimal Lévy searches for sparse, revisitable target sites; expected prey distributions in the region appear consistent with this (prediction 1) (see Discussion). Along the route taken by the shark in open shelf and shelf-edge waters, where dives sometimes exceeded 700 m, prey is assumed to be sparsely distributed because there are no reports of regular white shark–prey aggregations from southern Australia to the Ningaloo Reef region at the time of year sharks move into the area (spring–early summer).

Shark 2 was tagged with a data-logging archival tag while free-swimming at North Neptune Islands in South Australia (in August) and was captured in a commercial gillnet near the Head of the Great Australian Bight (GAB) in November (Fig. 2; Table S1). Using light-level-based estimates of longitude together with the depth profile during the tracking (Bruce, Stevens & Malcolm 2006), it appears this shark remained in the vicinity of the North Neptune Islands from 21st to 29th August before entering the shallower waters of the Spencer Gulf (transition between section 1 and 2; Fig. 2). The shark remained in the Spencer Gulf until 16th October (transition between sections 3 and 4) when it moved into deeper water and headed west into the GAB. This movement pattern was evident in other satellite-tracked white sharks tagged at the North Neptune Islands (Fig. S2). Vertical movements of shark 2 in section 1 approximate Brownian motion, predicting optimal behaviour for when prey is abundant (prediction 3). Indeed, these Brownian movements

occurred near to the North Neptune Islands, which is Australia's largest seal colony and thus an area of abundant prey for white sharks. Shark 2 moved into and remained in the Spencer Gulf for over 1 month, and then into the GAB, displaying ballistic movements within the Lévy range (sections 2 and 3), an optimal strategy for locating sparse, non-revisitable targets (prediction 2). The area of the Spencer Gulf is a wide region of low seabed complexity where commercial fisheries target prawn and finfish (e.g. snapper, Sparidae). Rays and skates are common by-catch in this area. In the GAB, commercial gillnets target gummy shark (*Mustelus antarcticus*). White sharks are known to feed on finfish (teleosts) and elasmobranchs in this region (Bruce 1992), and fishers in both Spencer Gulf and the GAB regularly report interactions with them; indeed, shark 2 was caught in a net set for *Mustelus*. Snapper are reported to form tight schools when moving through the lower central Spencer Gulf areas where shark 2 resided for over 1 month. Fishers further report loss of snapper school integrity over time when white sharks are present, suggesting that their predatory activity may result in the eventual dispersal of the school and hence a non-revisitable resource. Elasmobranchs, such as gummy sharks and rays, are likely to be in lower relative abundance and, as fast-moving prey, may therefore disappear readily, by employing high escape speeds, or in the case of rays by burial in the bottom substrate. The prey characteristics predicted from the observed search pattern appear consistent with the expected prey fields.

Shark 3 was fitted with a PSAT and an Argos satellite transmitter (Table S1) off Port Stephens in central New South Wales, and the detached PSAT tag was recovered after washing ashore near the Noosa region of Queensland (Fig. 3). The Port Stephens region provides a seasonal nursery area for juvenile white sharks from spring to mid-summer, where individuals remain in a highly localised area of coastal and adjacent shelf waters for weeks to months (Bruce & Bradford 2011). Shark 3 only remained in this region for about 8 days after being tagged (section 1) before moving into the open ocean (section 2), then moving back onto and northwards along the shelf into Queensland waters (section 3). After the PSAT tag detached, shark 3 was tracked (via SPLASH tag) returning south past Port Stephens and on to a second known nursery area off Corner Inlet, Victoria. Results of the analysis predicted movements linked to sparse prey in sections 1 and 2 (prediction 1), whereas in section 3, support for both Lévy and Brownian models for respective data sets was found. It is evident that white shark foraging behaviour is complex and in this case does not entirely confirm predictions. The Port Stephens region, including the adjacent shelf, is an area of high productivity and high finfish abundance (Lee *et al.* 2007; Bruce & Bradford 2011). White sharks when resident in the nursery area move between coastal reefs in mid-shelf waters and the nearshore surf zone, and their behaviour suggests periods combining active predation and rest where feeding is opportunistic (Bruce & Bradford 2011). This may explain why we found good model support for the truncated power-law model (prediction 1)

even though abundant prey aggregations were nearby, because most diving movements were not centred on this area (the surf zone). In section 2, the occurrence of optimal Lévy search ($\mu = 2.01$) predicted the presence of sparse prey that can be revisited or regenerated perhaps by aggregation (prediction 1). The satellite track of shark 3 shows movement into the deep ocean during section 2 where sparsely distributed prey is expected (Zainuddin *et al.* 2006). In section 3, mutual support for either model (truncated Lévy, exponential) was evident (Table S2), indicating complex behaviour during northward travelling along the shelf. This may reflect passing through habitats with both abundant and sparse prey.

Shark 4 was fitted with a PSAT tag and an internal acoustic transmitter (Table S1) off Port Stephens in November, where it spent the next 2 months (sections 1 and 2), prior to moving south past a line of acoustic receivers off Sydney on 15 January. Following this, the shark travelled consistently south (section 3) to the seasonally occupied, nursery area off Corner Inlet (section 4) in eastern Victoria where the PSAT detached and washed ashore (Fig. S1). Trackings of other white sharks tagged in the Port Stephens region, including shark 3 (Fig. 3), show similar movement patterns (Bruce & Bradford 2011) (Fig. S3). Analysis of vertical patterns within the known nursery area (sections 2 and 4) predicted the presence of abundant prey (prediction 3), which is confirmed by described productivity events, field observations of prey schools (see shark 3) and, in the case of Corner Inlet, the focus of commercial fisheries for snapper and elasmobranchs. The pattern of vertical displacements in section 3 was less clear with both the truncated Lévy and exponential models being supported for respective data sets, each across similar data ranges (Table S2). Although not yielding a clear prediction, white sharks travelling along the shelf might be expected to feed opportunistically on less aggregated prey than that present in residency areas.

Discussion

The great white shark is a large marine predator that feeds on a wide variety of prey including pelagic and demersal bony fish, various other sharks and rays, invertebrates, such as squid, and marine mammals, such as pinnipeds, cetaceans and cetacean carrion (reviewed in Bruce 2008). White sharks are observed to capture prey during periods of residency at certain locations interspersed with directed, sometimes prolonged, periods of travelling, presumably in response to the abundance, availability and behaviour of prey species (Bruce 2008). For example, white sharks may remain at, or at least visit regularly within a season, large and stable aggregations of prey such as seal colonies on isolated islands, e.g. off the coasts of California and South Africa (Martin *et al.* 2005). In addition, they feed on finfish aggregations in coastal habitats (Bruce 1992). White sharks have also been shown to travel long distances between potential prey aggregations both within coastal and shelf seas (Bonfil *et al.* 2005) and across the open ocean to oceanic islands (Jorgensen *et al.* 2010), between which times they likely search in a probabilistic

manner for prey in lower concentrations. It is the combination of this behaviour of white sharks to feed on abundant, aggregated prey sources occurring in predictable locations, with their propensity to make travelling excursions into more resource sparse locations, that presented us with the opportunity to test aspects of the LFF hypothesis (Viswanathan *et al.* 2011).

Our results show that white sharks exhibit vertical movements consistent with optimal Lévy flights at certain times and appear to switch between different patterns in relation to changes in their environment linked to resource distribution and availability. Other patterns also occur at other times, perhaps linked to more deterministic behaviours such as thermoregulatory movements, orientation and navigation. Similar conclusions linking movement pattern to resource distribution have been reached recently for other species of pelagic predator including other shark species, tunas and billfish (Humphries *et al.* 2010) and seabirds (Bartumeus *et al.* 2010). However, the current study undertakes a novel test by making predictions about probable prey abundance and characteristics encountered by white sharks based entirely upon quantitative analysis of movements; we then compared these predictions to the known prey types and relative abundance of white shark prey present in the habitats they occupied. Overall, we found that diving patterns during longer distance travel on the open continental shelf, shelf edge or in the open ocean, where prey is in lower abundance than around seal colonies and seasonal fish aggregations, were approximated by Lévy flights with exponents near the theoretical optimum for searching for sparse prey in revisitable patches (Table 1). It is not known precisely what white sharks feed on during such travelling behaviour. However, their general propensity to travel over depths consistent with relic coastlines in shelf waters or making deep dives (surface to 400–500 m; exceptionally down to 900 m), sometimes with a diel component when in slope and offshore waters, suggests opportunistic searching for either reef-associated species or those associated with deep scattering layers, respectively (Bruce & Bradford 2011), where relatively large-bodied squid may be the targets. Diel vertical migration (movement) (DVM) by sharks, tunas and billfish has been shown to be associated with scattering layers in several studies (Sims *et al.* 2005; Bernal *et al.* 2010). The Lévy and Brownian patterns we identify for white sharks occur in addition to DVM, because DVM is a pattern that occurs at a particular temporal scale or domain, nested within the scale-invariant structure of vertical Lévy flights (Sims *et al.* 2008).

An exception to this general pattern of Lévy flight behaviour occurring in open continental shelf, shelf-edge or open ocean habitats was evident in this study for shark 3, travelling northwards (section 3), and shark 4, travelling southwards (section 3), along the southern east coast of Australia. Interestingly, for both sharks travelling in open shelf habitats in this same geographic region, vertical movement patterns were equally well supported for both Lévy and exponential models. Clearly, this prevented us making a clear (single) prediction, but the similarity of this result between two similarly

sized sharks of the same sex and in the same region indicates that movements described by both models may have occurred. It is possible that abundant and sparse prey may be encountered by white sharks travelling along the shelf with its diverse habitats (from tropical to temperate). This could explain why we were unable to resolve each movement pattern component across the relatively long temporal scale of the time-series sections we used because sharks may switch frequently between search patterns in heterogeneous habitats (Humphries *et al.* 2010).

In contrast, for tagged white sharks showing localised horizontal movements consistent with a pattern of residency in an area with known abundant, temporally stable prey aggregations, quantitative analysis of vertical movements generally gave patterns approximated by Brownian motion (Table 1). Fine-scale localised movements made during hunting for seals can account for a pattern approximated by Brownian motion even though the geographic occurrence of seals was generally predictable. This is because Brownian motion is generally described by an exponential distribution where move-step lengths observed have a characteristic scale (mean) and finite variance (Viswanathan *et al.* 2011), such as that expected where movements are related to area-restricted searching or station-keeping behaviour where movement lengths occurring in a time series are likely to be of similar magnitude. We did not predict correctly that shark 3 (section 1) was resident in an area with high abundance of prey (e.g. seasonal aggregations of fish) off Port Stephens (Table 1), instead predicting near optimal Lévy searches. However, this white shark did spend less time near the surf zone where fish aggregate than in the open shelf environment (max. dive depth = 133.5 m) where prey may be encountered more opportunistically and where Lévy-type searches may be advantageous. Another exception to our general observation of Brownian movements in prey-abundant coastal areas was for shark 2. We predicted from ballistic Lévy movements within the Lévy range (Fig. 2) that prey would be non-revisitable, i.e. they may be more prone to escape or to hide without subsequent detection. It was evident from reconciling the vertical patterns with geographic locations for shark 2 that when exhibiting ballistic Lévy movements, it was residing in the shallow waters of the Spencer Gulf where prey aggregations occur but where they may hide, or where the activity of sharks may disperse finfish aggregations. Theory suggests that ballistic Lévy movements within the Lévy range present a more efficient strategy under these environmental conditions (Santos *et al.* 2004). Therefore, taken together, the empirical results of this study provide general support for the LFF hypothesis in so much that the vertical movements observed occurred in the habitats where they might provide – at least theoretically and at certain times – an optimal strategy for searching for the prey types and distributions known to be present there.

Reliable testing for the presence of Lévy flights in animal movement data requires large data sets to sample a power law thoroughly if it is present so as to increase the chances of detecting it from other types of distribution. Similarly, identi-

fying behavioural signals in time-series data is also enhanced if patterns analysed are less noisy, i.e. they have fewer interspersed behaviour types having different patterns. In this study, we used a large data set of over 1.2 million white shark movement steps. Nevertheless, each tag was retrieved prior to the end of its maximum scheduled deployment time due, in each case, to some form of tag attachment failure or physical removal from the shark prior to scheduled release. The archival tag on shark 2 was retrieved prematurely because the shark was captured and died in a gillnet. However, for sharks 1, 3 and 4, only between 24 and 60% of data scheduled to be recorded was collected prior to tag shedding. The reasons for premature shedding of PSAT tags were less clear for these sharks, but did not appear related to the swimming behaviour; rather, biofouling of tags may have played a role and is known to be a key factor in electronic tag failure on marine species (Hays *et al.* 2007) (see Data S1, Supporting information).

In addition to a large data set, we used split-moving window analysis to locate more consistent sequences of behaviour. However, while the majority of sections we analysed gave unequivocal support for one model over the other tested, two sections gave ambiguous support for both truncated power-law (Lévy) and exponential (Brownian) distributions (Tables 1 and S1). These sections have rank-step length plots of more complex form which may account for the less clear model selection. In support of this, a previous study demonstrated from simulations that rank-step length plots with similar complexity to those here can result if the data consist of both Lévy walks and Brownian motion (Humphries *et al.* 2010). Therefore, it seems that the foraging movements of white sharks may be similarly complex and reflect more rapid changes in behaviour type than could be detected with the statistical approach used. Field observations of the highly flexible predatory behaviour of white sharks appear to confirm this possibility (Martin *et al.* 2005).

Given the logistical difficulties of identifying what prey the tracked predators are feeding upon and what the actual distribution and abundance patterns of prey are in the natural environment (Makris *et al.* 2006; Sims *et al.* 2006), clearly several aspects of our results remain tentative. For instance, can it be assumed with certainty that white sharks making directed horizontal movements are actually searching for prey during vertical movements? Directed movements such as those seen by white sharks in this study may be movements between core, albeit distant, areas of a large home range, or they could be classified as migrations. Broadly speaking migration is an undistracted, population-level movement during which responses to resources such as food are generally suppressed (Dingle 1996). It is not certain whether white sharks feed during these long-distance transits, and it has been hypothesised that diving during directed movements might be related to navigation behaviour (Bonfil *et al.* 2005; Jorgensen *et al.* 2010). However, other species of large pelagic fish feed during apparent migrations (e.g. southern bluefin tuna *Thunnus maccoyi*; Bestley *et al.* 2008) and diving

movements characteristic of foraging have also been recorded during migrations of leatherback turtles *Dermochelys coriacea* (Hays *et al.* 2006), for example. On balance, it seems likely that white sharks also search and feed opportunistically during such longer distance movements. Our results for white sharks during travelling certainly support the idea that movements consistent with optimal Lévy searches are being conducted.

In some locations occupied by tagged white sharks, prey type and relative abundance have been documented. This is evident for shark movements near seal colonies and in areas where commercial fisheries operate (e.g. Spencer Gulf, south east Victoria and the GAB). Prey are abundant in those locations, and white sharks seem to respond by exhibiting Brownian-type vertical movements. A more complete knowledge of prey distributions in both shelf and open ocean waters inhabited by white sharks is, however, required. Details of stomach contents of white sharks captured in the oceanic environment are generally absent, but the deep diving behaviour we and others (Weng *et al.* 2007; Jorgensen *et al.* 2010) have observed does indicate some association with the deep scattering layers and perhaps with squid, a known prey item of white sharks (Bruce 2008). It is also possible that, when travelling, white sharks feed on tuna or cetaceans because their areas of occurrence certainly overlap. Large-scale maps of squid and tuna spatial abundance have only recently been estimated world-wide, but they indicate areas of higher than average abundance off south-west and south-east Australia (Tittensor *et al.* 2010), which is where Lévy searching during open shelf or open ocean travelling was observed. Although the white sharks were in global hot-spots for these oceanic species, available data indicate prey are sparsely distributed across vast areas. Area occupancy maps of tracked southern bluefin tuna over several months in oceanic habitat off south-west Australia (Bestley *et al.* 2008) indicate patchily sparse distributions. Furthermore, research survey and longline fishery data show that tuna distributions in both shelf and oceanic environments appear sparse across broad scales, from 100 to 2000 km (Zainuddin *et al.* 2006). Additionally, these prey locations are not as predictable as the abundant prey around seal colonies, for example; rather, oceanic fish prey appears largely unpredictable in its location not only in relation to oceanographic features such as fronts but within these areas from 1 year to the next (Sims & Quayle 1998; Zainuddin *et al.* 2006). The contrast between this sort of prey distribution in shelf and open ocean habitats and prey locally and predictably available at coastal seal colonies may explain, at least in part, the clear differences we observed between vertical movement patterns of white sharks in these two different habitats (coastal vs. shelf or open ocean).

A potential problem with interpretation of the current analysis might also be that the model fits obtained may be largely dependent on water depth. For example, an exponential distribution of vertical move-step lengths may have been found to be the best fit simply because the shark was diving in shallower water where longer steps were curtailed. Equally, it

is feasible that only Lévy (heavy tailed) distributions only occurred in deep water where longer vertical steps were possible. However, we found truncated Lévy flights in shallower waters on the shelf for several sections, including for shark 1 (section 4, max. depth 100 m), in addition to support for exponentially distributed move steps over a similar range in another shark (shark 4 sections 2 and 3, max. depths 125 and 150 m, respectively). This indicates that the effect of water depth in determining the modelled distributions cannot be considered a principal factor. Instead, the results suggest that it is the relative frequencies of occurrence of short, medium and long steps irrespective of depth that defines the form and gradient of the rank-step length plot and, hence, the best model selected.

Our results provide the first demonstration of predator movements approximating optimal Lévy flights and Brownian motion in natural environments where the search patterns present appear to be the most efficient for encountering the prey types known to be hunted there. There was congruence between our predicted prey characteristics (distribution, abundance and availability) from movement analysis and the known prey types and likely distributions in the habitats occupied by white sharks. One interpretation of these results is that white sharks show Lévy flight-type movements as an adaptive response to sparse prey fields, which may occur between areas of higher relative prey abundance. However, in addition to the presence of adaptive behaviours, the observed Lévy movement patterns could feasibly be an emergent property of a simple interaction between a white shark and its environment. For example, if prey were distributed according to a fractal (scale-invariant) distribution, as has been suggested for zooplankton and fish (Makris *et al.* 2006; Sims *et al.* 2006) for instance, then if a predator moved in straight lines between prey capture, it is probable that a Lévy flight pattern could emerge as a consequence of the distribution of prey and not due, *a priori*, to the adaptive behaviour of the predator (Boyer *et al.* 2006). However, while this seems a plausible alternative explanation for the results found here, there is evidence that individual animals show Lévy flight behaviour under controlled conditions in the absence of external cues (e.g. Cole 1995; Maye *et al.* 2007), which argues for the presence of innate behaviour patterns approximating Lévy flight. Furthermore, a recent study using quantitative genetic analysis to examine the mechanisms underlying the behavioural decision of an invertebrate (*Caenorhabditis elegans*) to leave a food patch showed genetic variation and environmental cues converge on common neural circuits to regulate this behaviour (Bendesky *et al.* 2011). This suggests that behaviours linked to decisions to make longer movement steps away from depleted food patches are heritable traits and not solely owing to simple interactions with food patches. Therefore, it is possible that the Lévy movement patterns we observed for white sharks represent flexible innate behaviours that have undergone natural selection and enhance the success of searching for prey. As such, our study may provide empirical support for the LFF hypothesis and the contention that organisms may have naturally evolved

behaviour patterns approximated by optimal Lévy random searches.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summary details of tracked white sharks.

Table S2. Summary of MLE and model selection results.

Fig. S1. Movements of white shark 4.

Fig. S2. Area occupancy of white shark 2 (boxes) compared with an Argos satellite track (blue circles and lines) of a different white shark similarly tagged at the North Neptune Islands (NN) seal colony.

Fig. S3. Area occupancy of white shark 4 (lines and numbers denote where vertical sections occurred) compared with an Argos satellite track (blue circles) of a different white shark similarly tagged at the Port Stephens (PS) aggregation site.

Data S1. Results and discussion.

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