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Effects of scale and habitat distribution on the movement of the southern stingray *Dasyatis americana* on a Caribbean atoll

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ABSTRACT: The structure of animal movement paths at varying spatial scales allows insight into the importance of habitat distribution and their response to scale in heterogeneous landscapes. Home-ranging animals typically exhibit constrained random movements at large spatial scales, with small-scale orientation reflecting responses to sensory stimuli. The southern stingray *Dasyatis americana* is an abundant demersal elasmobranch found in coastal systems throughout the Caribbean, yet very little is known of its movement ecology. Twelve southern stingrays were manually tracked at Glovers Reef (Belize) for up to 32 non-continuous hours to evaluate movement structure and activity space. Response to spatial scale was analysed using fractal analysis, and domains of scale were compared to habitat spatial characteristics. Mean stingray activity space was relatively small (<0.5 km^2) with daytime activity space significantly larger than nighttime activity space. Movement paths showed significant straightening correlated with increasing size in females. Stingray movement structure exhibited 2 distinct domains: at scales of <100 m, paths were more dispersed than a correlated random walk (CRW), and at scales >100 m, paths were more constrained than CRW, indicating directed movement at scales up to 100 m. Nearest neighbour spatial analysis of lagoon patch reefs showed mean spacing of 100 m (±4.5), equivalent to orientation distance seen in rays. Random walk movements at large scales are consistent with a home-ranging animal; however, larger scale orientation than expected and patch reef spacing equalling 100 m suggests that patch reefs represent important spatial and ecological networks, strongly influencing stingray movement, habitat use, and dispersal.

KEY WORDS: Acoustic telemetry · Correlated random walk · Fractal analysis · Movement · Spatial ecology · Spatial scale patterns

INTRODUCTION

Spatial ecology can drive population level processes with a similar effect to that of mortality, predation and competition (Pickett & Cadenasso 1995, Hanski 1998), hence the search strategy employed by an animal is crucial to success and efficiency in terms of overall fitness. Furthermore, examining animal movement patterns with respect to scale and structure of heterogeneous landscapes can provide key insights into their influence on biodiversity (Tilman 1994), population viability (Laidre et al. 2004) and metapopulation dynamics (Hanski 1998, Turchin 1998). The mode of movement utilised by a searching animal can significantly affect dispersal distance and distribution, with directed or orientated movements resulting in highly heterogeneous distributions compared to random and correlated random walks (CRW) (Hein et al. 2004). Without *a priori* information regarding the goal of a moving animal, discovering

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orientated movement is complex. Benhamou (2004) developed a statistical test based on the idea that the squared net displacement of a moving animal will increase linearly with number of steps if the movement mode is a correlated random walk, and quadratically if it is a directed walk (orientated movement). The ability to orientate over large distances has been observed for centuries in marine organisms such as turtles, whales and fish that return to natal or spawning grounds. However, the analysis of movement structure in relation to spatial scale and environmental homogeneity is relatively novel in the marine environment, having increased with technological advancement and greater precision of acoustic telemetry (Lowe & Bray 2006).

Animal search patterns represent a combination of movement processes (Bartumeus et al. 2005) that reflect foraging within, and at scales greater than the range of sensory perception (Papastamatiou et al. 2011). Higher resolution spatial data and fractal analysis (Nams 2005, 2006) allow us to identify changes in movement mode in response to landscape and scale, known as spatial domains (Wiens 1989). The precise structure of movement paths and the spatial scales at which animals change between directed to random walks provide important insight into drivers of movement and dispersal (Nams 2005, 2006).

Animals have been seen to orientate to specific habitat types (Zollner & Lima 1999a); towards stimuli from sensory receptors (smell, taste; Gardiner & Atema 2010); or towards certain locations, such as a burrow or den (Jamon & Benhamou 1989). The attraction to such a focal point or resource formed the basis of mechanistic theories of home range formation (Börger et al. 2008). Animals orientate at small scales when goals are within sensory detection range, whereas animals exhibiting orientated movements at large spatial scales are likely to be locating patches (areas of greater energetic return or reduced predation risk), through memory and experiential learning (Van Moorter et al. 2009).

Searching organisms increase the chance of encountering and capturing prey, and not being prey themselves, through the selection of foraging grounds or habitat (Stephens et al. 2007). As such, an animal will move within the smallest area that will satisfy its energetic and reproductive requirements (Mitchell & Powell 2004); this area, or a defined percentage over various temporal scales (e.g. 95%), is considered to be the home range (Grubbs 2010). A cognitive map of a home range, or of key features within it, is theoretically likely to increase foraging efficiency (Van Moorter et al. 2009) by reducing commute time between foraging patches, thereby conserving energy and lessening predation risk (Papastamatiou et al. 2011).

Despite the influential role demersal batoids can have in driving prey population dynamics (Dale 2011) and structuring benthic ecosystems through bioturbation (Thrush et al. 1991, Lohrer et al. 2004, O'Shea et al. 2011), very little is known about their movement patterns and response to landscape scale and structure. Directional and non-directional movement modes have been detected in bat rays *Myliobatis californica* moving along a linear embayment (Klimley et al. 2005), thought to be a behavioural thermotaxic response to water temperatures inside and outside the bay (Matern et al. 2000). Additionally, the manta ray *Manta alfredi* displays straighter movement paths within patches of high plankton prey abundance compared with more tortuous movements at larger spatial scales (Papastamatiou et al. 2012).

The southern stingray *Dasyatis americana* (Hildebrand & Schroeder 1928) is a large bodied, demersal stingray commonly found throughout the Western Atlantic from New Jersey to Brazil (Bigelow & Schroeder 1953, Aguiar et al. 2009). *D. americana* is an opportunistic mesopredator with a wide trophic niche (A. Tilley unpubl. data), preying predominantly on crustaceans and polychaetes (Randall 1967, Gilliam & Sullivan 1993). We used manual acoustic telemetry to explore diel movement patterns and activity space of *D. americana*. We predicted high site fidelity while utilising relatively large activity spaces, due to limited resource availability in low relief soft substratum (Lowe & Bray 2006). We hypothesised that movement structure would exhibit home-ranging characteristics of random walks with small scale orientated movements reflecting prey searching using sensory mechanisms. We used CRW models and fractal analysis of movement path structure to answer the following questions: (1) Do southern stingrays exhibit orientated movements, and if so to what scale? (2) Does southern stingray movement structure change according to spatial scale? (3) How do movement patterns relate to habitat distribution, and what can this tell us about stingray habitat use and search strategy?

MATERIALS AND METHODS

Study area

Glovers Reef Atoll (16.8° N, 87.8° W) is the southernmost of 4 coral atolls in the Mesoamerican Barrier

Reef System, situated approximately 40 km east of the Belizean coast, and 20 km east of the main barrier reef. The atoll covers approximately 254 km^2, most of which is made up by the lagoon, surrounded by a reef crest. The lagoon is approximately 27 km long and 10 km wide, with a maximum depth of 20 m, and fringed by a sand apron extending inward from the reef crest to a depth of ~2 m, and a flattened shallow lagoon comprised of sand, seagrass meadows and algal fields amongst rugose patch reefs to a depth of ~5 m (Fig. 1). *Dasyatis americana* is present in the lagoon in very high densities (~245 rays km^{-2}) throughout the year (Tilley & Strindberg 2012), and is not currently targeted by fisheries, hence it provides an ideal location to study natural movements of a wild stingray population in an isolated system.

Acoustic tracking

Twelve *Dasyatis americana* were captured and tagged within the lagoon margin of Glovers Reef Atoll at 2 sites, A and B (Fig. 1). At Site A, 8 rays were encircled individually with a gill net between June 2009 and April 2010, then brought into an onboard tank where size (curved disk width; DW) and sex were recorded. Acoustic tags were crimped to a monofilament loop passed through the tail musculature using a hypodermic needle (adapted from Le Port et al. 2008). Pit tags were injected into right side dorsal musculature to identify individuals and avoid duplication. Handling times did not exceed 10 min and rays were released at the capture site and monitored in-water after release for periods of up to 30 min to ensure recovery. At Site B, 4 rays were tagged in-water using a modified dart tag applied by pole spear into the dorsal musculature in the saddle area. These rays were located by boat or with swimmers; a snorkeler then approached from directly behind the ray to insert the dart tag with the pole spear. Size measurements were estimated post-capture by measuring the width of feeding pit or resting 'footprints' left by tagged rays during foraging (footprints were validated by comparing measured values from 3 other captured individuals with their in-water values. In-water measurement error was <3 cm across all individuals).

All rays from Sites A and B were tagged with a continuous acoustic transmitter (V9/V13 Vemco Systems) with a signalling interval of 2 s on one of 7 frequencies (60, 63, 66, 75, 78, 81, 84 kHz). A hull-mounted V110 directional hydrophone connected to a VR100 or VR60 acoustic telemetry receiver (Vemco Systems) was used to track V9/V13 transmitters. Range tests carried out with both receiver units and tag types prior to tracking found maximum detection ranges of 400 to 600 m in depths of >0.5 m, yet reduced to less than 100 m in water of <0.5 m. No tagged rays moved into water shallower than 0.5 m during tracking. V9 tags were used for the first 6 rays tracked, then changed to V13 tags (due to their longer battery life) for the remaining 6 rays.

Tagged rays were left to return to normal behaviour for at least 24 h before commencement of track-

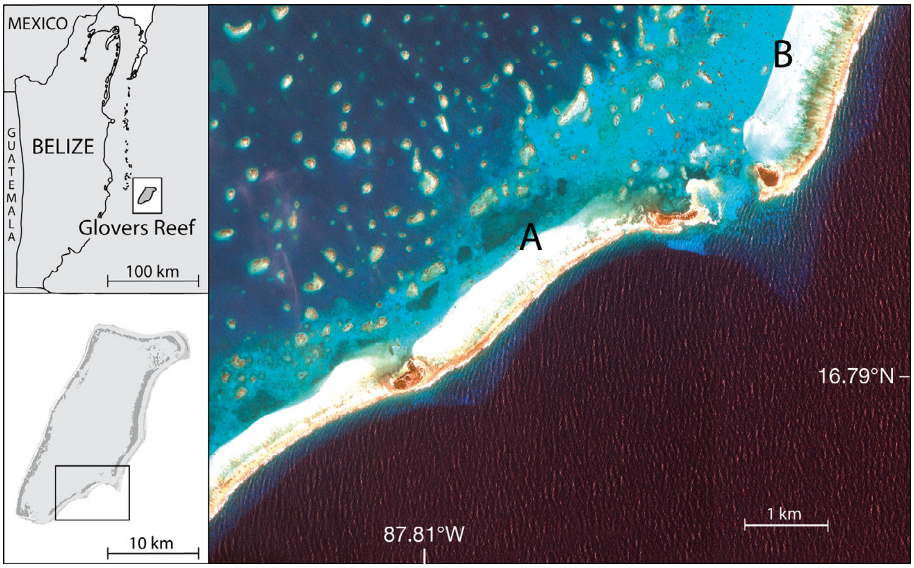

Fig. 1. Study area at Glovers Reef Atoll, showing location within Belize (top left panel), a map of the Atoll (lower left panel), and an enlarged satellite image of the study site (main panel) with tagging locations (marked as A and B)

ing. Rays were tracked non-continuously for a total duration of between 1 and 24 d covering all diel phases, with a minimum continuous tracking period of 4 h and a maximum of 24 h. Ray locations were recorded every 5 min using handheld and VR100 built-in Global Positioning System (GPS). A distance of >10 m was maintained between boat and animal in order to minimize disturbance of the rays' natural movements.

Tracking data analysis

Locations of tracked stingrays were plotted using ArcMap (ArcGIS, ESRI 9.3) laid over a georeferenced IKONOS satellite image (4 m resolution) of the south east section of Glovers Atoll, in order to analyse stingray activity space and net displacement (defined as the direct distance between start and end points of each movement path) through the diel cycle. Local sunrise and sunset times were used to classify the diel phase during the tracking period for each individual ray (total annual variation of ±4 min).

Total and diel activity spaces were calculated using Kernel Density Estimation (KDE), local convex hull (LoCoH) nearest neighbour convex hull (Getz & Wilmers 2007) and minimum convex polygons to produce 50 % (core area) and 95 % isopleths of utilisation. KDE utilisation distributions were calculated using proportions of an optimum reference bandwidth (h_{ref}) taken from a Gaussian kernel (Home Range Tools (HRT) Ver. 1.1 Rodgers & Kie 2010). Polygons created from 50 % and 95 % density isopleths using proportional h_{ref} values were compared post hoc to LoCoH and minimum convex polygons (MCP) to find the most suitable activity space estimate for the distribution of location points for individual rays. Total, daytime and nighttime activity spaces were compared using a Wilcoxon test, and analysed against stingray individual size and sex using regression analysis and Wilcoxon 2-sample tests, respectively.

Five minute interval step lengths were extracted from stingray location data using HRT (Rodgers & Kie 2010). Data were analysed using a restricted maximum likelihood mixed model (JMP 9, SAS Institute) to explore effects of diel period (hour, night and day) and individual variability on stingray movements.

Fractal analysis

Movement paths were analysed using Fractal Software version 5 (V. Nams, Nova Scotia Agricultural College). Stingray net displacement was compared to computer-generated CRW models using the CRW_{diff} statistic described by Kareiva & Shigesada (1983) and adapted by Nams (2006):

$$\text{CRW}_{\text{diff}} = \frac{1}{k}\sum\nolimits_{n=1}^{k} \frac{\overline{R_n^2} - E(R_n^2)}{n^2\,\bar{l} - E(R_n^2)} \qquad (1)$$

where $\overline{R_n^2}$ represents the observed mean (net distance)^2 for each number of consecutive moves; $E(R_n^2)$ is the expected mean (net distance)^2, $\bar{l}$ is the mean step length, and k is the turn angle concentration. Computations were carried out at 200 spatial scales along the track to generate an overall estimated value of CRW_{diff} for each individual. The minimum step size for the analysis was set at 10 m to allow for level of inaccuracy of location data, and bootstrapping was set to a mean of 1000 replications. Values of CRW_{diff} less than zero suggest movements are more constrained than a CRW, implying random walk movements (Nams 2006). This test assumes that a ray orientating to a feature would have greater displacement at large spatial scales than a CRW, because it is moving towards the goal as directly as the environment will allow (Nams 2006).

Fractal dimension (Fractal *D*) of movement paths was measured using the divider method to calculate the tortuosity at differing scales back and forth along the length of the path using multiple replications. Fractal *D* is measured on a scale of 1 to 2, where 1 is a straight line and 2 is a path so tortuous as to cover a 2D plane (Nams 2006). Mean Fractal *D* was used as an indicator of tortuosity for individual rays, and following log(Fractal *D*−1) transformation, was analysed against individual size and sex using regression and ANOVA tests, respectively, performed in JMP9 (SAS Institute). The sections of spatial scale exhibiting a constant movement structure are termed 'domains', and 'transitions' describe the point at which movement structure changes (Wiens 1989). VFractal (Nams 2006) was used to calculate Fractal *D* at different spatial scales to highlight transitions and domains of movement structure (Nams 2005). If animal movements are spatially homogeneous, Fractal *D* and variance will increase steadily with scale. A decline in Fractal *D* with increasing scale equates to a straightening of movement paths. Calculation of the variance of Fractal *D* with spatial scale allows for identification of domains, as variance will be highest at the transition between intense searching and more dispersive movements. Correlation of Fractal *D* between successive path sections tests for patch use irrespective of search strategy, as no patch use would exhibit a zero correlation at all scales. Positive correlations show scales smaller than patch size, negative at patch size, then increasing back to zero as scale gets much larger than patch size (Nams 2005).

Habitat analysis

In-water observations were made of the area through which stingrays were tracked to analyse habitat characteristics and to ground-truth satellite images. A georeferenced IKONOS satellite image (4 m resolution) of the study area was used to analyse spatial characteristics of the southeastern portion of Glovers Reef lagoon using ArcGIS. Nearest neighbour distance analysis (Hawth's tools extension for ArcMap) was used to assess patch reef spacing within the cumulative activity space utilised by all acoustically tracked stingrays. Patch reefs >5 m in diameter and rising to <1 m below the surface of the water were analysed for distance from their closest 3 neighbouring patches within the cumulative stingray activity space, and the mean distance calculated.

RESULTS

Activity space and net displacement

Seven female and 5 male *Dasyatis americana* were tracked sporadically throughout the diel cycle for periods ranging between 1 and 24 d, and continuous animal tracks lasted between 4 and 24 h (Table 1). Hours tracked in daytime and nighttime were approximately equal for each ray. KDE isopleths of 95% total activity space ranged from 0.16 to 0.79 km^2 with a mean (±SD) of 0.42 ± 0.19 km^2. There was no significant correlation between activity space and days ($r^2 = 0.012$, $p = 0.74$, df = 11) or total hours tracked ($r^2 = 0.1$, $p = 0.32$, df = 11). No significant relationships were seen between size of ray (DW) and total activity space ($r^2 = 0.27$, $p < 0.09$, df = 11), daytime activity space ($r^2 = 0.29$, $p < 0.07$, df = 11), or nighttime activity space ($r^2 = 0.035$, $p = 0.56$, df = 11). Furthermore, when activity space was compared between size classes (males <48 cm and >48 cm DW, females <75 and >75 cm DW following Henningsen 2000), no significant differences were seen in overall activity space (Wilcoxon 2-sample $Z = 0.16$, $p = 0.81$), daytime activity space ($Z = 0.16$, $p = 0.81$) or nighttime activity space ($Z = 0.49$, $p = 0.63$). Nighttime 95% activity space (median 0.22 km^2) was significantly smaller than 95% daytime activity space (0.29 km^2) (restricted maximum likelihood (REML) $F = 7.46$, $p < 0.0195$), with individual variability accounting for 43% of the model variance. Core activity spaces (50%) showed no significant difference in size between day and night (Wilcoxon $Z = -1.59$, $p = 0.06$) and accounted for a very small proportion of mean (±SD) total area (17.1 ± 10.7%) (Fig. 2). Mean core activity space for rays was 0.07 ± 0.04 km^2. Further, no significant differences were seen between sex and total activity space (Wilcoxon 2-sample test $Z = -0.83$, $p = 0.40$), daytime activity space ($Z = -0.97$, $p = 0.33$), or night-

Table 1. Acoustically tracked *Dasyatis americana* (n = 12) at 2 locations (A & B in Fig. 1) in Glovers Reef Atoll, Belize between June 2009 and July 2010. '95% All' values refer to total activity space calculated from all locations of each individual ray. CRW$_{diff}$ reflects the p-values from statistical testing of path displacement compared to a correlated random walk model (values in **bold** represent paths significantly less constrained than a CRW). Patch size values reflect the scale at which largest correlation of tortuosity (Fractal *D*) was seen in fractal analysis

Ray ID	Date tagged	Location	Tracking period (d)	Total hours tracked	Sex	Size (DW mm)	95% all (km^2)	95% day (km^2)	95% night (km^2)	CRW$_{diff}$ p-value	Mean Fractal *D*	95% CI	Patch size (m)
DA1	23 Aug 09	A	7	24	F	310	0.155	0.137	0.07	**0.006**	1.489	1.349–1.628	45–70
DA2	23 Aug 09	A	9	30	F	650	0.849	0.788	0.308	**0.03**	1.256	0.959–1.553	50–90
DA3	09 Sep 09	A	4	24	F	770	0.625	0.441	0.262	**0.08**	1.264	0.882–1.647	55–85
DA4	11 Oct 09	A	3	24	F	435	0.689	0.393	0.284	**0.004**	1.493	1.115–1.872	65–95
DA5	11 Oct 09	A	24	27	M	335	0.31	0.192	0.038	**0.01**	1.189	1.091–1.288	50–85
DA6	15 Nov 09	A	3	24	M	530	0.341	0.235	0.107	**0.003**	1.438	1.177–1.700	60–80
DA7	12 Feb 10	A	7	26	F	290	0.293	0.188	0.253	**0.02**	1.555	1.322–1.788	50–80
DA8	16 Apr 10	A	19	32	F	700	0.463	0.355	0.089	**0.02**	1.263	1.161–1.365	67–90
DA9	05 Jul 10	B	3	22	M	520	0.43	0.241	0.348	**0.001**	1.228	1.178–1.278	130–200
DA10	14 Jul 10	B	7	26	M	450	0.4	0.327	0.322	0.2	1.268	1.043–1.493	40–80
DA11	24 Jul 10	B	1	24	F	860	0.446	0.346	0.156	0.09	1.303	1.114–1.491	65–87
DA12	26 Jul 10	B	1	22	M	550	0.335	0.244	0.263	0.3	1.184	0.082–2.286	35–100

time activity space ($Z = 0.49$, $p = 0.63$). The data were explored for seasonal patterns, but given the low sample size, there were not enough to represent each season, and no significant effects emerged.

Step length distribution was significantly different between hour periods (REML $F = 3.95$, $p < 0.0001$) (Fig. 3). Five percent (SE = 139.2) of model variation was accounted for by between-subjects variance in modelling step length and hourly period.

Correlated random walk

Between 4 and 7 tracks were analysed for each individual ray. Of tracked individuals, 75 % ($n = 9$) showed significantly greater displacement than a CRW (CRW_{diff} values are shown in Table 1).

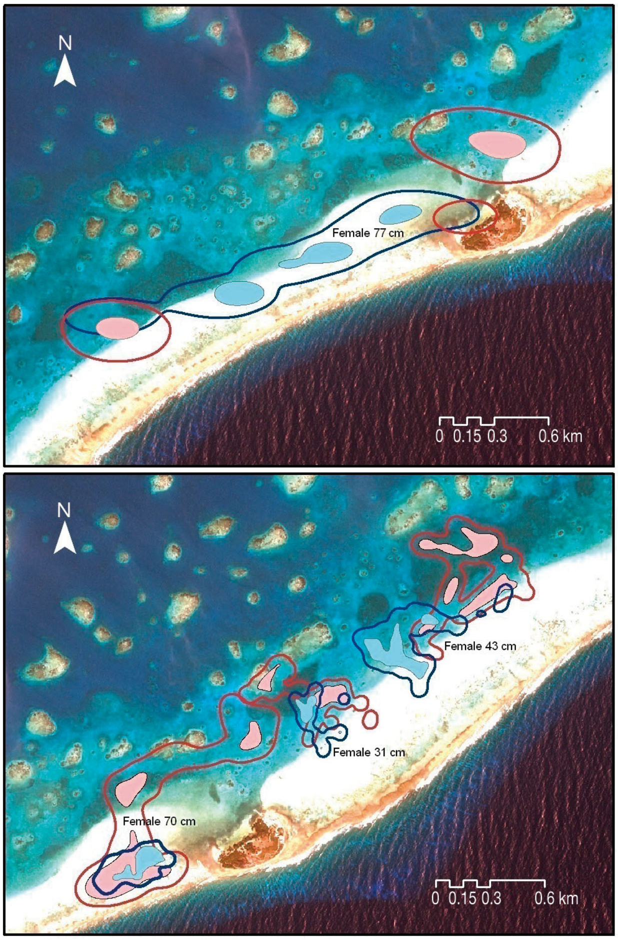

Fig. 2. Examples of diel activity spaces of 4 *Dasyatis americana* at Glovers Reef Atoll, Belize. Dark blue isopleths indicate 95 % night areas with core 50 % use areas shaded light blue. Daytime 95 % areas are outlined in red with core 50 % use areas in pink

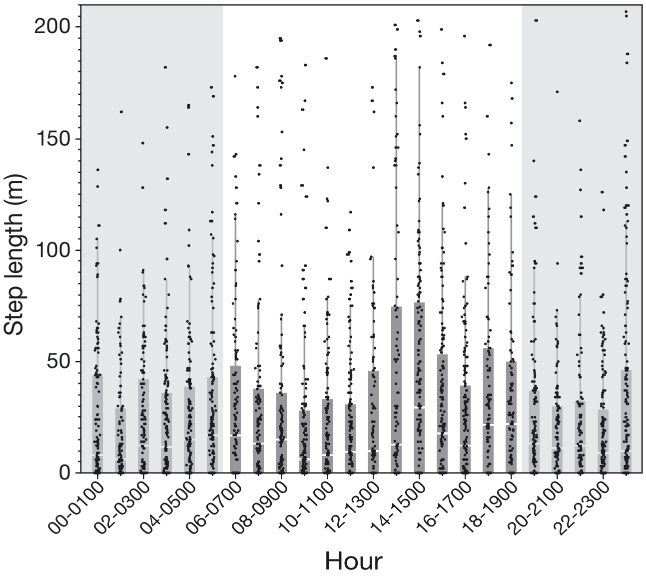

Fig. 3. Five-minute interval step-lengths binned by hour for 12 *Dasyatis americana* tracked over a diel cycle in Glovers Reef Atoll, Belize. The 2 shaded areas represent night periods. Boxplots represent lower, median and upper quartiles, with bars depicting 95 % confidence intervals

Domains of scale and tortuosity

Individual mean Fractal *D* showed no significant correlation with male size ($r^2 = 0.11$, $p = 0.58$, $s = 0.38$), yet exhibited a significant negative correlation with female size ($r^2 = 0.69$, $p = 0.02$, $s = 0.25$) indicating larger females moved in straighter movement paths than smaller females (Fig. 4).

Fractal *D* and variance for all rays pooled, continuously increased with scale showing no spatial heterogeneity until ~95 m, where there was a discontinuity indicating a domain of scale and change in movement structure (Fig. 5a–b). Variance peaked at 117 m, indicating a transition. Narrow confidence intervals suggest all rays moved with similar patterns.

Analysis of orientation of stingray movements

Ray movement paths showed significantly greater dispersal than CRW at spatial scales <100 m (Fig. 6). At spatial scales >100 m, dispersal decreased to negative values compared to a CRW.

Individual rays showed a large degree of variation in dispersal patterns over spatial scales. CRW_{diff} was positive at scales of up to 100 m for 71 % of individual rays tracked.

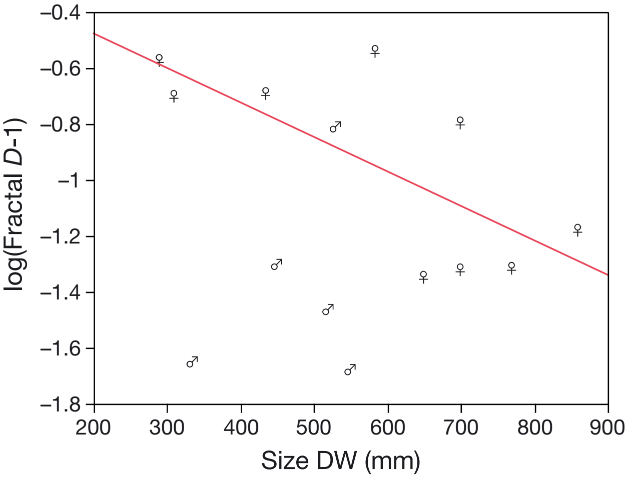

Fig. 4. Mean path tortuosity (Fractal *D*) exhibited by size of *Dasyatis americana* (n = 12). Tortuosity values of female movement paths (♀, solid red line) show a significant negative correlation with individual size. Male values: ♂

Habitat spatial analysis

Stingray movements were restricted to the lagoon fringe habitat, equating to a depth range between 1 and 6 m. Patch reefs were predominantly located in the deeper lagoon margin (>2 m) and were immediately surrounded by a ring of clear sand, free from the surrounding seagrass cover. Patch reefs exhibited varying degrees of rugosity and coral cover, from sparse rubble patches to 5 m coral and algal towers. Only patch reefs of 5 m diameter and <1 m below the water surface were included in nearest neighbour analysis. The distances between all patch reefs and their 3 nearest neighbours (n = 123) ranged from 33 to 293 m. The mean nearest neighbour distance (±SE) was 100 m (±4.5).

DISCUSSION

Diel movements and activity space

Stingrays were tracked over multiple days, and for the most part were found to be associated with the same patch reefs, or within 100 m of where the previous tracking phase had ended. *Dasyatis americana* activity space was small (0.42 ± 0.19 km^2) and the regularity with which rays could be found over weeks and months, within the same area implies strong site fidelity (A. Tilley unpubl. data).

Diel movement patterns relating to activity space and step length differences suggest rays are more active in the daytime, though high individual variation in diel activity space highlights the need for more data. Preliminary work from the Cayman Islands suggests large adult *Dasyatis americana* heighten

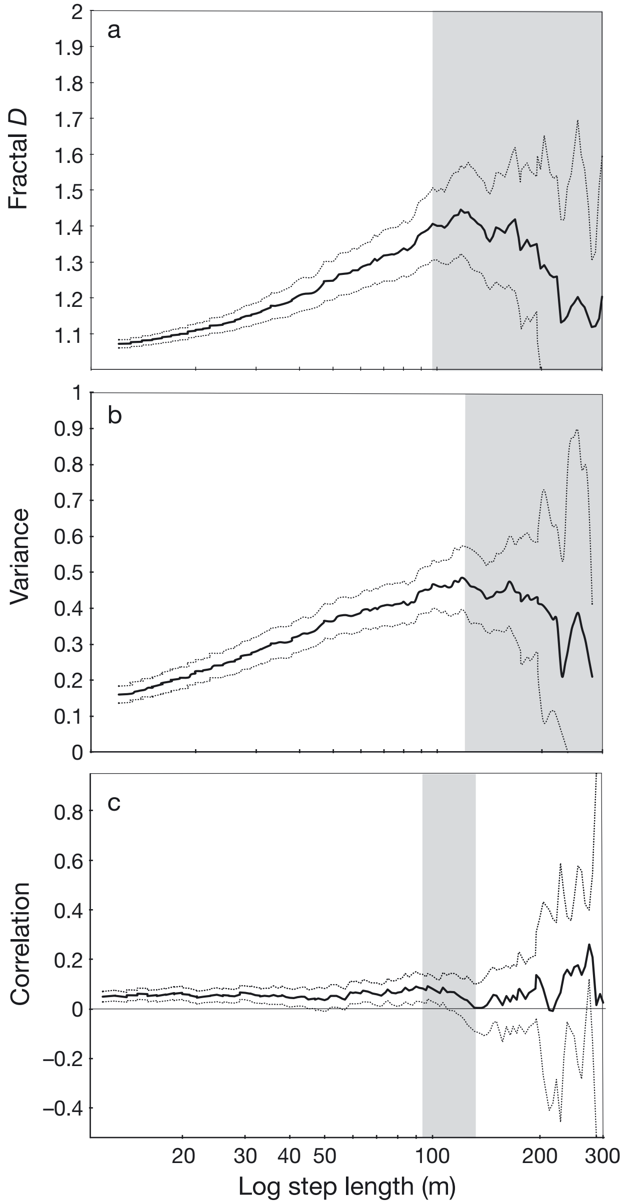

Fig. 5. Fractal analysis for *Dasyatis americana* movement patterns at Glovers Reef Atoll. (a) Fractal *D*, (b) variance of tortuosity and (c) correlation of successive segments are plotted against log spatial scale for all tracked rays combined (n = 12). Solid black lines: mean values; dotted lines: upper and lower 95% confidence intervals. Shaded boxes indicate transitions between domains of scale in movement structure. The peak in tortuosity at 100 m (a) indicates a change in stingray movement structure at that scale. A negative correlation at 100 m (c) indicates patch use, with a peak in variance at 120 m (b) suggesting a maximum patch size

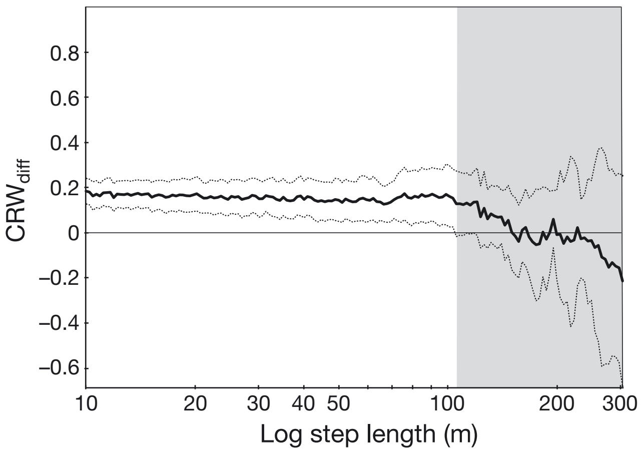

Fig. 6. Combined analysis of orientation for *Dasyatis americana* (n = 12). Orientation is seen to a scale of ~100 m, where lower confidence limits of dispersal drop below that of modelled correlated random walk (CRW_{diff}, grey shaded area). Solid black line: mean value; dotted lines: upper and lower 95% confidence intervals

activity at night (Corcoran 2006), such as illustrated in Fig. 2, possibly reflecting nocturnal foraging behaviour as seen in many coastal elasmobranchs (McKibben & Nelson 1986, Wiens 1989, Holland et al. 1993, Cartamil et al. 2003, Vaudo & Lowe 2006, Chapman et al. 2007, Collins et al. 2007). The lack of clear distinction between diel periods may be a factor of the continued and opportunistic foraging behaviour of *D. americana* (Bigelow & Schroeder 1953, Randall 1967, Gilliam & Sullivan 1993), where individual changes to peak activity periods may respond to local environmental factors such as predation risk. Caribbean reef sharks are known to enter the Glovers Reef lagoon at night (Chapman et al. 2007) and other sharks may behave similarly. Hence, large rays may be less vulnerable to predators at night than sub-adults and juveniles, and therefore may maintain activity at night.

Fractal and spatial analysis

Stingrays exhibited orientated movements at scales <100 m, indicating directed walks to known goals. Movement at scales >100 m was indicative of a random walk. Stingrays may orientate using memory of their home range up to a scale of 100 m from experiential learning, combined with inherent environmental cues such as depth and vertical habitat diversity. The transition between 2 spatial domains and orientation distance of stingray movement corresponded very closely to spatial attributes of the lagoon habitat dotted with rugose patch reefs, with a mean (±SE) spacing of 100 m (±4.5), and daytime field observations show rays utilising clear sand areas around patch reefs for foraging and cryptic burial. Patch reefs are likely to provide multiple benefits to rays such as: reducing predation risk (Heithaus et al. 2002, Aguiar 2003, Smith et al. 2008); increasing prey availability at the reef/sand interface (Lowe 2002, Mitchell & Powell 2004, Gratwicke & Speight 2005); or for behavioural interactions such as cleaning (Snelson et al. 1990). Field observations of rays refuging within the patch reef structures in the presence of sharks (D. Chapman pers. comm.), and following tagging procedures (A. Tilley pers. obs.) support the use of patch reefs in evading predation. The use of topography or complex structures for refuge reflects findings by Strong et al. (1990), where *Dasyatis americana* fled into a submerged wreck in the presence of a great hammerhead shark.

Directed walks within foraging patches can indicate orientation to potential prey stimuli (Papastamatiou et al. 2009). Orientation at very small scales (<0.5 m) in batoids is likely to be in range of mechano-sensory systems such as touch (Montgomery & Skipworth 1997), and electro-sensory systems (Haine et al. 2001, Montgomery & Walker 2001). Environmental circumstances may significantly affect sensory ability, yet it is understood that under appropriate conditions, olfaction, hearing and vision operate at greater distances. Without precise knowledge of stingray visual and olfactory ability, and range of perception, it is difficult to understand the role of direct sensory cues as a driver of stingray orientation, and hence whether orientated movements occur only within prey patches. Stingrays are likely to be visually vigilant due to dorsal eye morphology (McComb & Kajiura 2008), however, even if visual perception hypothetically extends to 100 m in rays, water clarity is likely to inhibit visibility (Semeniuk 2004) at this range. Elasmobranch olfaction is sensitive to amino acids at extremely low concentrations (Meredith & Kajiura 2010), and may drive direct movements in rays from a distance of ~100 m, if the stimulus is a continually diffusing source, such as fish or conch remains. Rheotaxis, or the upstream swimming response following chemical stimulation is seen in many shark species (Mathewson & Hodgson 1972, Peach 2002), and nurse sharks *Ginglymostoma cirratum* have been shown to orientate to chemical gradients even without current (chemo-klinotaxis; Hodgson & Mathewson 1971). Naturally emitted odorants from common prey classes such as decapods, bivalves and crustaceans (Bigelow & Schroeder 1953, Randall 1967, Gilliam & Sullivan 1993) are unlikely to be sufficient for rays to trace from a distance in a wave-disturbed environment (Kotrschal 2000). Further experimental work testing the sensory mechanisms in rays will be necessary to estimate detection range with regard to prey types.

Dasyatis americana moved in a very narrow depth band of 1 to 5 m in the lagoon margins. Due to the linearity of reef environments, it might be argued that perceived orientation is in fact movement according to spatially structured depth gradients, as seen in blacktip reef sharks (Papastamatiou et al. 2009). Movement along this apron edge could be used for orientation throughout home ranges 3 km in length, but this would not account for a diminished orientation by rays at a greater scale than 100 m, as found when compared to a CRW. Ray selection of foraging patches (at scales >100 m) may not be a random walk, but rather a larger CRW or directed walk constrained by home range mechanisms such as focal point attraction. Various models have been suggested to account for the emergence of animal home ranges, yet lack of a general mechanism remains a fundamental problem in movement ecology (Börger et al. 2008). Home range behaviour may account for stingrays' ability to orientate at scales up to 100 m as a result of experiential learning of landmarks and key topographical features, as illustrated with homing wood mice (Jamon & Benhamou 1989). This observation implies that rays may use the distribution of patch reefs as a network of refuges, connected by pathways of potential foraging areas. Stingray use of patch reefs for orientation within their home range would support recent suggestions that home range formation increases foraging efficiency, and that memory systems are key in the emergence of home range behaviour (Van Moorter et al. 2009). Moreover, there is evidence to suggest that memory builds home range from heterogeneous patches (Van Moorter et al. 2009), rather than animals first selecting home ranges, then choosing the habitats to use therein as had been previously suggested (Sallabanks 1993). Similarly, Stamps (1995, p. 41) suggested that animals 'may learn site-specific serial motor programs that enhance their ability to move rapidly, safely, and efficiently around obstacles and barriers in familiar areas.' At scales greater than 100 m, ray movement was not significantly different from a CRW suggesting that although movement within and between patches appears to be directed, selection of foraging patches is more random, as has been shown with mice (Benhamou 1991) and manta rays (Papastamatiou et al. 2012).

Individual size of female rays was negatively correlated with mean path tortuosity, indicating that larger, older rays used straighter movement paths which reflects previous findings for basking sharks (Sims et al. 2006) and thresher sharks (Papastamatiou et al. 2011). Computer simulations suggest straighter movement paths are more efficient than tortuous random searches (Zollner & Lima 1999b) implying that learning and experience enhance the ability to perform directed walks. The lack of a clear pattern to support this theory for males may suggest greater sampling, of a wider size range, is needed. Furthermore, this may have additional significance as more direct movements by larger individuals may represent a response to reduced predation risk through a size refuge. Further information on predator abundance and prey behaviour according to habitat would be required to test such responses, as exemplified in Heithaus et al. (2009).

A mean value for tortuosity (Fractal *D*) was calculated from entire paths, and could be construed as a bias of greater sample size at larger spatial scales; where large rays travel greater distances, expanding activity space in a linear environment. However, this is unlikely as the mechanics of fractal geometry dictate the opposite; Fractal *D* naturally increases with the scale at which paths are viewed (Wiens 1989, Nams 2005), where longer paths (if scale invariant) will display a gradually higher value of Fractal *D* (i.e. more tortuous) than shorter, scale invariant paths. This again may present a situation of sensory perception vs. memory as the facilitator for orientation, as straighter movement paths seen by adult female rays could suggest they possess more developed sensory mechanisms (i.e. greater perception range), or that learning and experience of their environment improves reference memory (Van Moorter et al. 2009).

Further work should attempt to identify relationships between the spatial distribution of resources and habitats (e.g. patch reefs) and home range size (i.e. with variations in spacing of patch reefs, and in fore reef habitats exhibiting only limited sand substrate) in order to understand the population level dispersal of these important marine mesopredators in heterogeneous environments. Additionally, greater understanding of the sensory capabilities of stingrays with regard to range of vision and olfaction would allow for greater insight into the dependence of these senses in foraging behaviour. To understand the relationship between stingray movement structure and home range, experimental work should be pursued with rays outside of their natural home ranges such as in Zollner & Lima (1997). Our study illustrates the utility of quantitative analytical tools in understanding batoid movement ecology, and demonstrates the importance of topographic habitat structure and distribution to these demersal predators.

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