

Home range of immature green turtles tracked at an offshore tropical reef using automated passive acoustic technology

Julia Hazel · Mark Hamann · Ivan R. Lawler

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Abstract Seventeen immature green turtles *Chelonia mydas* were tracked concurrently by automated ultrasonic receivers at a coral reef off North-Eastern Australia (September–December 2010, 16.4°S, 145.6°E). The majority ($n = 11$) were tracked for the entire 100-day study, the remainder for 23–85 days. Detection data aggregated at 30-min intervals produced median 6.5–35 daily locations for individual turtles. Home range areas (95 % utilisation distribution) were $\leq 1 \text{ km}^2$, $\bar{x} \pm \text{SD} = 0.74 \text{ km}^2 \pm 0.159$. To the best of our knowledge, these are the first home range estimates for *C. mydas* foraging at offshore tropical reefs. The findings are important for conservation in revealing near-continuous presence of the same individuals within a small geographic area. Time between detections was very short (median < 3 min) demonstrating passive ultrasonic technology can track multiple turtles in a foraging environment with higher temporal resolution than typically achieved by satellite tracking.

Introduction

Marine turtles have attracted expanding research effort over recent decades (Awise 2008; Godley et al. 2008), but

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J. Hazel · M. Hamann · I. R. Lawler
School of Earth and Environmental Sciences, James Cook
University, Townsville, QLD 4811, Australia

J. Hazel (✉) · M. Hamann
Centre for Tropical Water and Aquatic Ecosystem Research,
Townsville, QLD 4811, Australia
e-mail: julia.hazel@jcu.edu.au

important knowledge gaps remain, including a paucity of data regarding turtles in their geographically diverse foraging areas (Bjorndal 1999; Hamann et al. 2010). This gap may seem surprising for the globally threatened green turtle *Chelonia mydas* (Seminoff 2004), given that they spend the major part of their lives in neritic foraging grounds (Musick and Limpus 1997; Plotkin 2003) and suffer multiple anthropogenic impacts at some foraging sites (Lutcavage and Lutz 1997; Hazel and Gyuris 2006). However, the data deficit might in part be explained by technology constraints.

Satellite tracking has effectively revealed long distance migrations by turtles (Godley et al. 2008; Hart and Hyrenbach 2010; Hazen et al. 2012), but fine-scale tracking studies are hampered by the relatively low spatial resolution of satellite-derived locations. Furthermore, even with enhanced accuracy offered by recent marine variants of GPS technology, temporal resolution of satellite tracking remains a fundamental constraint (Hazel 2009). The problem is particularly acute for turtles in foraging areas because they spend the vast majority of time submerged (Hazel et al. 2009). During submergence, no satellite-derived locations can be obtained because radio signals necessary for satellite communication are blocked by seawater (Hill and Robinson 1962); therefore, researchers need to consider other methods for fine-scale tracking of submerged animals.

Ultrasonic acoustic signals transmit effectively over short distances underwater and allow active boat-based tracking with a directional hydrophone. This is a labour-intensive technique because the tracking boat follows one animal at a time, and work is further constrained by weather and sea conditions (e.g. Mendonca 1983; Zeller 1997; Holland et al. 1999; Seminoff and Jones 2006). Newer technology offers vastly expanded scope for passive tracking with omni-directional receivers capable of detecting many coded transmitters on a single ultrasonic frequency. These automated receivers

can be deployed as fixed arrays in diverse situations (see review by Heupel et al. 2006). Prompt adoption and widespread studies attest to the utility of this new technology in fish research (e.g. among many others Heupel and Simpfendorfer 2005; Yeiser et al. 2008; Knip et al. 2011; O'Toole et al. 2011). In contrast, there has been sparse and limited usage for marine turtles where (i) ultrasonic signals were interpreted simply as turtle presence or absence near a particular receiver and the detection data were not used for calculating geographic position estimates (see Simpfendorfer et al. 2002); (ii) additional methods supplemented the ultrasonic data, e.g. Taquet et al. (2006) incorporated systematic diver observations, Okuyama et al. (2010) relied in part on depth recorders, Hart et al. (2012) relied primarily on satellite tracking. Thus potential utility of this technology as a stand-alone method for turtles has remained difficult to assess.

The present study had two objectives: (i) to estimate home ranges of green turtles foraging at an offshore coral reef by means of automated ultrasonic receivers and (ii) to report in detail on performance of the receiver array. Achievement of objective (i) would constitute the first step in alleviating a wide data gap of conservation importance. More than 2000 offshore coral reefs exist within Australia's Great Barrier Reef (Hopley et al. 2007). Many of these reefs host substantial foraging aggregations of green turtles (Chaloupka and Limpus 2001) implying such coral reefs collectively represent significant habitat for the species. However, prior to the present study, no spatial ranges could be found for green turtles foraging at Australian offshore coral reefs, nor for this species in similar habitat elsewhere in the world. Objective (ii) was expected to assist other turtle researchers in assessing the potential utility of automated ultrasonic tracking for future studies.

This paper uses the term 'home range' in a broad sense to describe the geographic extent of turtle movements recorded during the study period. Quantitative measures (detailed below under *Home range measures*) were pragmatic choices based on recommendations in scientific literature. We acknowledge diverse alternatives and ongoing debate regarding the definition, calculation and reporting of home range measures (e.g. see Laver and Kelly 2008 and references therein). Such debate lies beyond present scope.

Methods

Field research

Low Isles (16.4°S, 145.6°E) is situated on the continental shelf of North-Eastern Australia and lies entirely within a Marine National Park Zone of the Great Barrier Reef Marine Park (GBRMPA 2004). Our study site comprised a small coral reef supporting a vegetated sand cay and a

mangrove cay connected by a shallow reef flat that is partially exposed at extreme low tides (Fig. 1). Boat searches of the reef flat were conducted at mid- to high tide in water depths 0.5–2.5 m, and green turtles were hand-captured by an assistant jumping from the boat. Each study turtle was released within 1 h after being processed onboard the boat close to the capture site.

Ultrasonic transmitters (V16-4L, Vemco, Halifax, Nova Scotia, Canada) were embedded in streamlined epoxy fairing and attached to the posterior carapace (Supplementary material Fig. S1) with epoxy adhesive-putty (Knead-It Aqua, Selleys, Padstow NSW, Australia) taking care to avoid obstructing the transducer end. The transmitters produced a coded signal with a nominal delay of 90 s, meaning that the interval between successive transmissions varied randomly between 60 and 120 s. A variable transmission rate was necessary to reduce the risk of signals from multiple transmitters being emitted concurrently. Signals overlapping in time can cause a form of interference termed 'signal collision' that prevents successful decoding (Manufacturer's advice, Vemco, Halifax, Nova Scotia, Canada.)

Underwater receivers (VR2W, Vemco, Halifax, Nova Scotia, Canada) were attached to concrete weights anchored to the substrate. Each receiver deployed in deep water was attached to a rope supported by a small sub-surface float, in order to maintain upright orientation. Receivers deployed at inter-tidal locations were supported in PVC tubes embedded in concrete weights and placed directly on the substrate (Supplementary material Fig. S1). The same locations, hereafter termed 'receiver-stations',

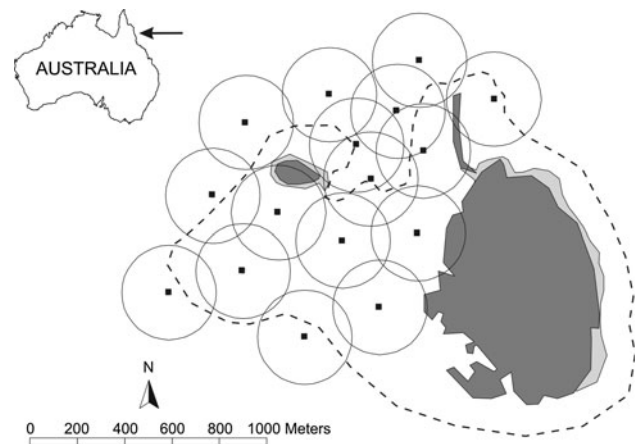


Fig. 1 Study site at Low Isles (16.4°S, 145.6°E) off the north-east coast of Australia. Dashed line indicates approximate extent of the coral reef complex that supports a small sand cay to the west and a larger mangrove cay to the east. Light grey indicates sand, dark grey indicates vegetation, small squares indicate locations of receiver-stations. Circles with radius 200 m allow visual evaluation of receiver-station spacing in relation to signal detection range tests presented in Fig. 2

were used throughout the study. The receivers operated automatically, constantly ‘listening’ for signals on the same ultrasonic frequency as the V16 transmitters and recording all signal detections in archival memory. Each receiver was brought to the surface at approximately 4-week intervals for cleaning and data download and promptly replaced.

Design of the receiver array was guided by range tests at the study site that showed a V16 transmitter within 50 m of a receiver produced near-perfect detection (99 %). More than 50 % of signals were detected up to 300 m, decreasing to 11 % detection at 300–400 m. (Fig. 2). Distances between adjacent receiver-stations varied (approx 200–350 m) to accommodate complex shorelines and to avoid placing

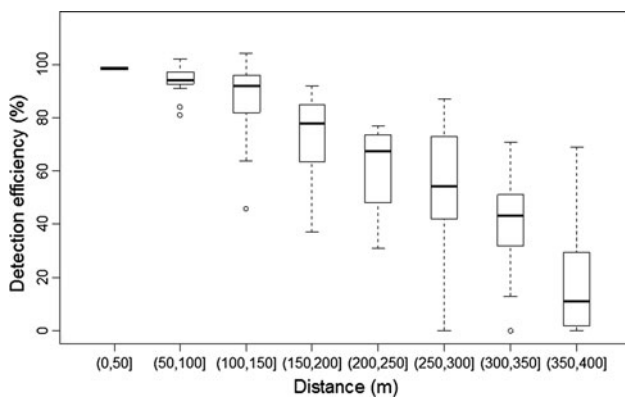


Fig. 2 Detections were recorded by submerged acoustic receivers (Vemco VR2 W) at various distances from an ultrasonic transmitter (Vemco V16) moored at a fixed location. Detection efficiency is presented here as the percentage of emitted ultrasonic signals that were successfully detected during range testing at the study site

equipment on coral or in boat transit lanes and high-use anchorage areas. Wave intensity prevented the placement of receivers along the southern and eastern edges of the reef (Fig. 1). Completion of a 15-receiver array defined the start of our 100-day study on 16 September 2010. An additional receiver was installed later (6 November 2010) at the most easterly position shown on the site map (Fig. 1). Data from this additional receiver-station were included in analyses of turtle activity but excluded from diagnostic metrics.

Data analysis: diagnostic data

Each VR2W receiver provided two types of data: (a) a list of transmitter signals successfully decoded, termed Detection data and (b) information relevant to efficient functioning of the receiver, termed Events data. We used Events data to calculate three diagnostic metrics: Code Detection Efficiency, Rejection Coefficient and Noise Quotient (Pincock 2008; Simpfendorfer et al. 2008; Vemco 2010) as defined in Table 1.

Data analysis: detection data

Successfully decoded signals were matched, via signal ID codes, to the turtle carrying the corresponding transmitter. For each turtle, we calculated tracking duration, number of days on which the turtle was detected, detections per day and elapsed time between successive detections. As an additional measure of receiver performance, total detections were standardised by the number of individual turtles detected on each day of the study.

Table 1 Events data recorded by passive underwater receivers (VR2W, Vemco, Halifax, Nova Scotia, Canada) were used to calculate three diagnostic metrics developed by the manufacturer

and expert users of the Vemco tracking system (Pincock 2008; Simpfendorfer et al. 2008; Vemco 2010)

Term	Definition	Value
<i>Events data</i>		
Ping	A single pulse transmission, forming a component of the 8-pulse sequence emitted by a V16 transmitter	P = 24 h total Pings
Sync	The time interval between first and second Ping in a transmitter sequence, a very specific value that differentiates a valid transmitter signal from unrelated pulses	S = 24 h total Syncs
Detect	A sequence of 8 Pings that had been successfully decoded	D = 24 h total Detects
Reject	A sequence of Pings with correct parameters that failed to pass a complex error checking algorithm	R = 24 h total Rejects
<i>Diagnostic metrics</i>		
Code detection efficiency	The ratio of daily Detects to daily Syncs	CDE = D/S
Rejection coefficient	The ratio of daily Rejects to daily Syncs	RC = R/S
Noise quotient	The difference between total Pings and number of Pings expected if each Sync had been followed by a complete sequence, where large positive or negative Noise Quotient values can indicate noise, echoes or collisions	NQ = P - (S × 8)

We used detection data for each turtle to estimate locations of centres of activity during successive 30-min time steps ($\Delta t = 30$) following Simpfendorfer et al. (2002). Coordinates of these locations were calculated as the arithmetic means of latitude and longitude for all receiver-stations detecting the turtle during that time step, weighted by the number of detections at each station. The same calculations were repeated with other time step values ($\Delta t = 5, 15$ and 60 min) to assess the influence of this parameter. If this comparison showed greater utility of a different time step, the initial pragmatic choice of $\Delta t = 30$ could be changed accordingly. Minimum straight line distance was calculated between consecutive locations and termed ‘continuous distance’ when there were no intervening periods of non-detection, or ‘interrupted distance’ when locations were separated by variable periods of non-detection. Displacement rate (distance/time) was calculated from continuous distances only. Local sunrise and sunset times were used to define day and night.

Home range measures

Utilisation distributions were estimated by the fixed kernel method (recommended by many authors e.g. Worton 1989, 1995; Kernohan et al. 2001). To avoid confounding our comparisons, we applied consistent kernel parameters across all data sets (fixed kernel smoothing, user-defined bandwidth and grid resolution). Utilisation distribution (UD) contours were used to depict each turtle’s range of activity in two-dimensional space with the 99 % contour (UD 99 %) interpreted as maximum recorded activity range during the study period, UD 95 % as the area of routine use, equivalent to ‘home range’ sensu Burt (1943) and White and Garrott (1990), and UD 50 % as the core area of activity. UD contours were plotted on a map of the study area for visual evaluation. Bhattacharyya’s Affinity statistic (Bhattacharyya 1943; Fieberg and Kochanny 2005) was used to quantify the degree of similarity between UDs estimated from locations at four different time steps ($\Delta t = 5, 15, 30, 60$ min). The Utilization Distribution Overlap Index (Fieberg and Kochanny 2005) was used to measure the degree to which individual turtles shared space. Our usage followed recommendations by Fieberg and Kochanny (2005) where detailed information and tests of the above statistics are provided. Calculations were conducted in R (R Development Core Team 2010) with package *adehabitat* (Calenge 2006) used for UDs.

Results

Nineteen green turtles with curved carapace length (CCL) from 65.5 to 80.6 cm were equipped with tracking

transmitters deployed in July 2010 ($n = 7$) and September 2010 ($n = 12$), of which 17 provided transmitter signals at the start of our 100-day study period (16 September 2010).

Tracking duration and detection frequency

Eleven of 17 available turtles were tracked throughout the 100-day study, five for more than half the period (51 to 85 d) and one for 23 d. Nine turtles recorded multiple detections each day without exception (detections $d^{-1} \bar{x} \pm SD = 209 \pm 87.8$). The other eight turtles were detected on 95–99 % of days within their tracking duration (detections $d^{-1} \bar{x} \pm SD = 88 \pm 42.1$). For all individuals, the time between successive detections was predominantly very short (median = 1.7 min, range <0.5 min to 8 days). Gaps in detection >24 h for 8 turtles collectively comprised 13 non-detection periods of 1–3 days, one of 6 days and one of 8 days. Table 2, Supplementary material Fig. S2.

Space use by study turtles

Detection data aggregated at 30-min time steps provided a per-turtle median of 1,599 locations, range 375 to 3,514 (Table 2). These locations indicated study turtles collectively used an area of 1.63 km² (UD 99 %) over the 100-day study period, with routine use (UD 95 %) of 1.22 km² and a core area (UD 50 %) of 0.29 km² in the North-West sector of the study site (Fig. 3). Individual turtles had home range areas (routine use UD 95 %) $\bar{x} \pm SD = 0.74 \text{ km}^2 \pm 0.159$, range 0.47–1.04 km² and core areas (UD 50 %) $\bar{x} \pm SD = 0.14 \text{ km}^2 \pm 0.043$, range 0.08–0.24 km². Individual utilisation patterns were diverse, as shown quantitatively by the Utilization Distribution Overlap Index (UDOI) median 0.43, range 0–1.87. UDOI values were consistent with qualitative evaluation of the utilisation maps (Supplementary material Fig. S3). For example, turtles A7 and A19 used geographically similar areas in accord with UDOI = 1.87, whereas A3 and A8 UDOI = 0 used geographically distinct areas. In the latter case, A3 favoured the eastern side of the study site and A8 favoured the west, and they overlapped only within their UD 99 % (Supplementary material Fig. S3, Table S1). Day and night utilisation patterns for individual turtles were geographically similar, but night areas were smaller than day areas, UD 95 % day-night difference $\bar{x} \pm SD = 0.15 \text{ km}^2 \pm 0.129$, UD 50 % day-night difference $\bar{x} \pm SD = 0.08 \pm 0.052$.

Receiver performance

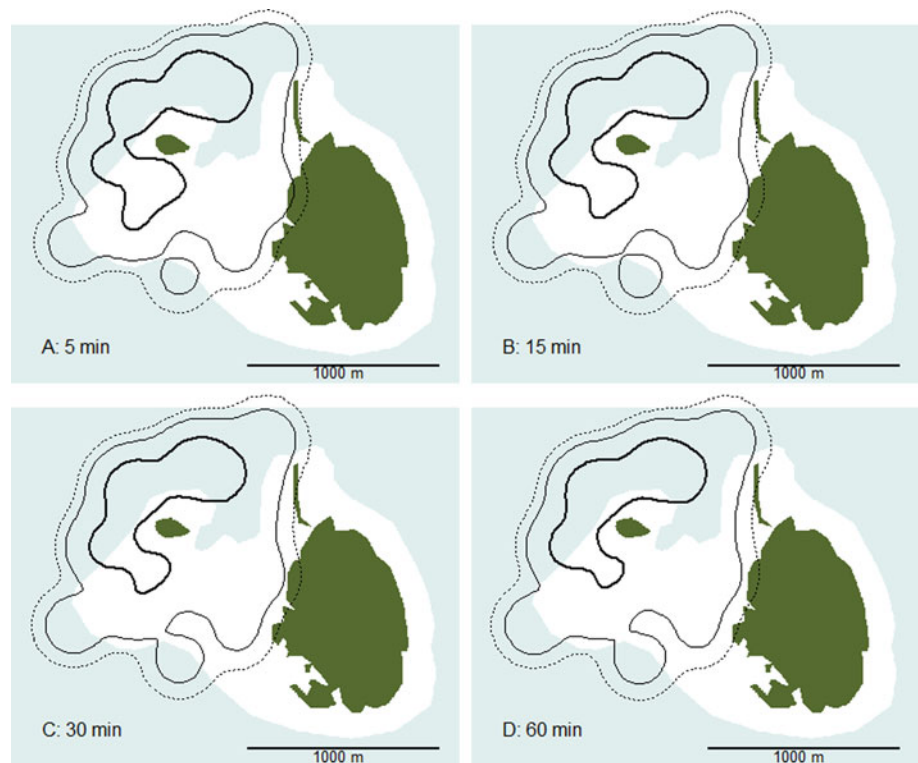
Receiver Event data showed the mean daily Code Detection Efficiency was 0.386 (median = 0.396, range 0–1) indicating that on average, less than 40 % of transmissions

Table 2 *Chelonia mydas*. Green turtles equipped with ultrasonic transmitters were tracked by an array of passive underwater receivers

Turtle	CCL (cm)	Overall tracking duration (days)	Study tracking duration (days)	Daily detection	Total signals detected	Time (min) between detections median [max]	Total locations for $\Delta t = 30$ min	Daily locations for $\Delta t = 30$ min (median [range])
A1	79.4	58	NA	NA	NA	NA	NA	NA
A2	71.9	124	59	98 %	6,404	1.9 [3,432]	1,252	20.0 [3–35]
A3	68.6	164	100	95 %	16,211	1.4 [2,483]	1,422	12.0 [1–45]
A4	65.5	125	60	100 %	12,962	1.6 [1,189]	1,458	24.0 [2–36]
A5	67.5	>164	100	100 %	18,786	1.7 [606]	2,600	25.0 [13–41]
A6	71.0	>164	100	100 %	19,510	1.8 [797]	2,907	29.0 [14–42]
A7	80.2	>159	100	98 %	2,613	2.8 [2,131]	777	6.5 [1–30]
A8	78.7	93	85	99 %	5,903	2.0 [1,592]	1,599	19.0 [2–35]
A9	77.8	30	23	96 %	2,692	1.8 [11,563]	375	22.0 [3–34]
A10	71.7	>108	100	100 %	36,950	1.6 [950]	3,514	35.0 [16–48]
A11	76.4	>107	100	100 %	14,438	1.9 [991]	2,590	26.5 [10–40]
A12	71.1	>107	100	100 %	14,704	1.9 [941]	2,911	28.5 [14–45]
A13	73.6	58	51	98 %	4,667	1.7 [1,449]	743	14.5 [1–22]
A14	76.1	>106	100	100 %	11,394	1.9 [827]	2,267	21.5 [13–43]
A15	76.7	>106	100	100 %	33,869	1.4 [816]	2,845	26.0 [8–47]
A16	80.6	106	100	100 %	17,228	1.5 [1,159]	2,182	20.0 [9–42]
A17	78.2	5	NA	NA	NA	NA	NA	NA
A18	75.5	65	60	97 %	5,642	1.9 [8,987]	977	23.5 [1–38]
A19	71.6	>106	100	95 %	7,332	1.8 [4,553]	1,457	15.0 [1–45]

Overall tracking duration was from transmitter attachment until the last signal detected prior to the defined end of the pilot study. Symbol “>” indicates additional signals were detected after the end date. All other values refer to the 100-day study period. Daily detection indicates percentage of days an individual turtle was detected within its study tracking duration. Minimum time between detections in all cases <0.5 min. Locations refer to weighted mean coordinates for 30-min intervals (Δt)

Fig. 3 *Chelonia mydas*. Utilisation distribution kernels 50 % (heavy line) 95 % (light line) and 99 % (dotted line) estimated for all turtles showed close similarity when based on activity centre locations calculated at four different time steps, 5–60 min, panels a–d



were successfully decoded over the 100-day study. However, the daily Rejection Coefficient was very low (mean = 0.017, median = 0.013, range 0–0.33), and Noise Quotient was generally moderate with occasional extreme values (first quartile = –252.0, mean = –112.7, median = –63.0, third quartile = 52.0, range = –2,449 to 1,793). Variation was irregular and sometimes high, but no consistent temporal trends emerged in any of the three diagnostic metrics (Fig. 4a–c). However, daily totals for signals detected (median = 1,992, range 1,048–4,712) showed an irregular but overall diminishing trend, evident in raw numbers and when totals were standardised by the number of turtles detected on each day Fig. 4d.

Influence of time step value

Increasing the time step value ($\Delta t = 5, 15, 30$ and 60 min) for calculating locations from detections progressively increased the proportion of time steps with locations

derived from one or more receiver-stations and reduced the proportion of time steps without detection. Increasing Δt increased the median distance between successive locations, as would be expected for consistency with longer elapsed time, but concurrently the inferred displacement rate decreased. Bhattacharyya's Affinity statistic $BA \geq 0.99$ for all pairs of comparisons indicated the utilisation distributions were very closely similar for the four Δt values although spatial areas of UD contours decreased slightly with longer time step values (Table 3, Fig. 3).

Discussion

Tracking duration and detection frequency

The majority of turtles (11 out of 17) remained in contact, via acoustic signal detection, for the full duration of the 100-day pilot study and only one individual ceased contact

Fig. 4 Performance data for the array of acoustic receiving stations ($n = 15$) over the 100-day study period. Three diagnostic metrics (defined in Table 1) indicated considerable variation but no consistent trends in **a** Code detection efficiency, **b** rejection coefficient and **c** noise quotient. *Box plots* show daily values for all receiver-stations pooled; *horizontal bar* indicates median; *box length* indicates inter-quartile range; *whiskers* extend to largest values within $1.5 \times$ inter-quartile range; all more extreme data points shown as open circles. Detections standardised **d** shows total signals detected standardised by the number of individual turtles recorded on each day

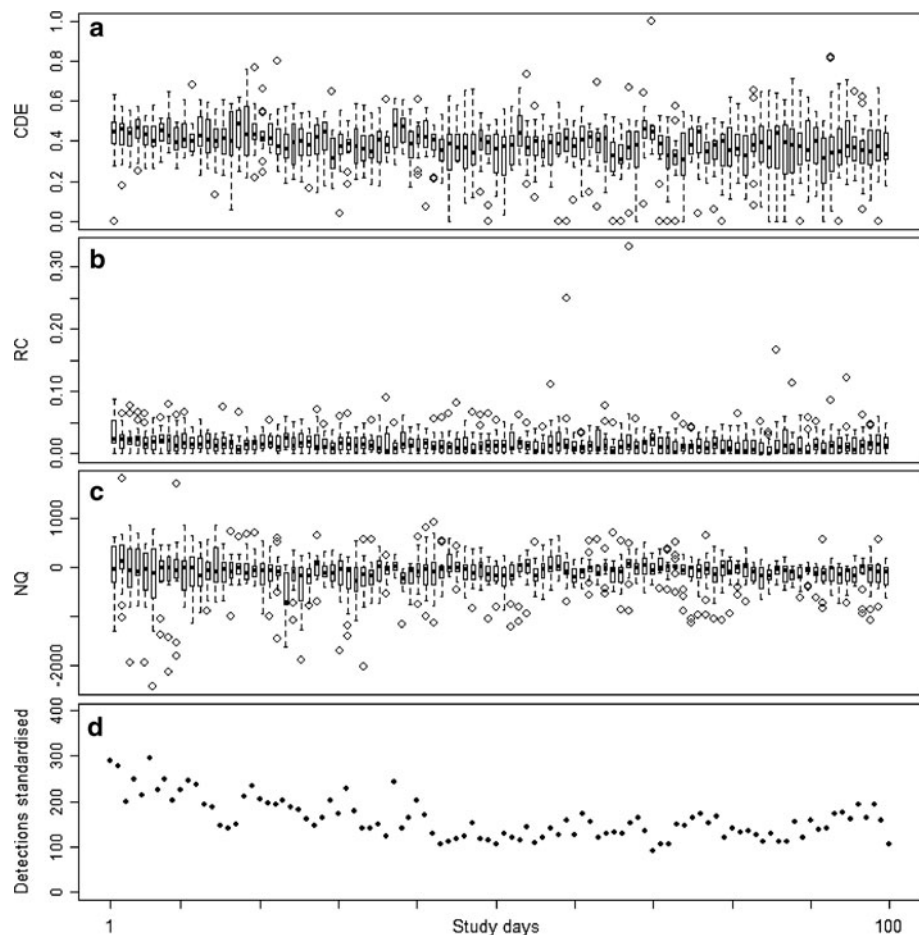


Table 3 *Chelonia mydas*. Comparison of four different time step values (Δt) applied for calculating locations from detection data for all study turtles ($n = 17$)

	$\Delta t = 5$ min	$\Delta t = 15$ min	$\Delta t = 30$ min	$\Delta t = 60$ min
Total locations	99,312	49,607	31,876	19,509
Detections per location (median [range])	2 [1–21]	3 [1–54]	4 [1–79]	6 [1–130]
Receiver-stations contributing detections (% of Δt intervals comprising 100 days)				
1	18.0 %	23.3 %	26.9 %	27.9 %
2	4.5 %	8.4 %	11.7 %	15.2 %
3	1.2 %	2.8 %	4.4 %	6.7 %
4	0.4 %	1.1 %	2.2 %	3.8 %
≥ 5	<0.1 %	0.6 %	1.4 %	3.5 %
None	75.8 %	63.7 %	53.3 %	42.9 %
UD 95 (km ²)	1.23	1.22	1.22	1.22
UD 50 (km ²)	0.32	0.30	0.29	0.28
Continuous distance (m) median [range]	0 [0–1013]	51 [0–1013]	62 [0–1013]	86 [0–1056]
Interrupted distance (m) median [range]	0[0–1409]	24 [to 1409]	119 [0–1378]	193 [0–1302]
Displacement rate (m s ⁻¹) median [range]	0 [0–3.38]	0.06 [0–1.13]	0.03 [0–0.56]	0.02 [0–0.29]

For details, see text *Data analysis: Detection data*. Continuous distance refers to consecutive locations without intervening periods of non-detection. Interrupted distance refers to consecutive locations separated by variable periods of non-detection. Displacement rate refers to continuous distance only

during the first half of the period. Study turtles were detected multiple times per day, either on every day ($n = 9$) or on 95–99 % of days ($n = 8$) indicating they maintained near-continuous presence at the small tropical reef complex at Low Isles.

Occasional non-detection intervals >24 h could have indicated brief departures from the study site or un-recorded movements within the site. We estimated that a return trip from Low Isles to another reef (the nearest 12 and 16 km distant) would involve at least 2 days of travel, based on mean swimming speeds <1 km h⁻¹ recorded for green turtles of similar and larger sizes in fine-scale tracking studies (Seminoff and Jones 2006; Brooks et al. 2009; Hazel 2009). Therefore, within the two longest gaps in detection (6 and 8 days), a potential excursion to another reef might hold relatively low foraging benefit relative to the turtle's energy expenditure for travel. Alternatively, detection gaps could have occurred if some turtles moved temporarily to southern or eastern parts of the Low Isles reef complex where their transmitter signals would have been out of range of our receivers. A more extensive receiver array would have been useful for reducing this ambiguity.

A premature end of detection for a minority of turtles might have been caused by active departure from the study area, or by turtle death (resulting in the carcass drifting away), transmitter failure, or transmitter detachment. Only the latter explanation has been confirmed. Two study turtles were re-encountered at the study site subsequent to the

tracking period. They were in good to very good body condition (see Heithaus et al. (2007) for visual assessment criteria) but had lost their transmitters. Close inspection of the carapace suggested transmitter loss was due to scute-shedding rather than adhesive failure (J. H. pers. obs). Data are lacking regarding scute-shedding by wild *C. mydas* at any life stage, thus it remains unclear whether natural scute-shedding might represent an important limitation for adhesive attachment. For the present study, we relied entirely on adhesive attachment (i) to avoid drilling the carapace for mechanical fastenings and (ii) to facilitate eventual safe shedding of equipment because recapture for manual removal was not assured at our site. For tracking studies of extended duration, other researchers might consider supplementing adhesives with bolts or wires, subject to ethical considerations and regulatory conditions.

Space use by study turtles

All study turtles used home range areas ≤ 1 km². These are to our knowledge the first home range estimates for green turtles foraging at an offshore coral reef and no prior data could be found for direct comparison. However, there is notable contrast between the small home ranges of turtles at Low Isles and larger ranges reported at various coastal sites: for example 3.5 km² over 22–51 days (Mendonca 1983, values for 'summer' periods of study), 3.2 km², over 4–26 days (Whiting and Miller 1998); 16.6 km² over 34–96 days (Seminoff et al. 2002), 2.4 km² over

55–66 days (Makowski et al. 2006) and 4.6 km² over 4.5 days (Hazel 2009).

Unlike coastal sites, the Low Isles reef complex is entirely surrounded by open water with depths 15–30 m (Australian Hydrographic Service 2002). Such depths do not preclude foraging or resting by green turtles at some locations (e.g. Taquet et al. 2006). However, we suspect only scant forage exists in deeper waters around Low Isles because seagrass is restricted by low light penetration in turbid water (Abal and Dennison 1996). The latter is an enduring characteristic of our study region due to high rainfall, terrestrial runoff and re-suspension of sediments (e.g. see Hamilton 1994; Larcombe and Woolfe 1999). In addition, this part of the continental shelf features gentle gradients without underwater reefs (Australian Hydrographic Service 2002). Consequently the surrounding open water lacks coral and rock outcrops that turtles at Low Isles evidently favour for resting (J.H. pers. obs). Therefore, we suggest a spatial concentration of forage and shelter resources within the reef complex at Low Isles may explain the small home ranges of our study turtles.

Within the study area, there was sparse seagrass and macro-algae scattered across the reef flat while coral outcrops along the reef slopes offered shelter for resting turtles all around the perimeter of the site (J.H. pers. obs.). Similar sparse forage and abundant rest sites were present in the North-West area that received higher use by study turtles considered collectively (see UD 50 % in Fig. 3). However, that area might have been slightly favoured by turtles because it was partly sheltered from prevailing South-East winds and swell. Clearly, there was no strong preference for any particular area, given that individuals had different core areas. Indeed, their diverse home ranges (Supplementary material Fig. S2) suggested each study turtle found its own optimal pattern of resource use within the Low Isles reef complex.

The finding that study turtles used slightly larger areas by day than by night was consistent with the understanding that green turtles tend to move about more widely while foraging during the day and tend to rest during much of the night. Evidence of diurnal activity and nocturnal rest has also been inferred from the diving patterns of green turtles (Seminoff et al. 2001; Hazel et al. 2009). However, our data did not show a geographic distinction between day and night sites, as has been reported in some situations (Mendonca 1983; Taquet et al. 2006). General similarity between areas used by day and by night at Low Isles may reflect site characteristics, because wherever a turtle forages within this site, it can find multiple potential rest sites nearby. In general, Low Isles turtles can be observed to rest intermittently during the day (J. H. pers. obs.) and might occasionally forage at night (not feasible to observe). Thus there was no expectation that turtles would use clearly differentiated areas by day and night, nor was the tracking

method designed to detect small differences in habitat use. Very precise locations cannot be obtained from ultrasonic detection data due to variations in detection efficiency (Fig. 2) and imperfect spatial coverage, notably around the perimeter of the array. Other methods should be considered for studies where geographic accuracy is the highest priority, for example standard GPS or Fastloc GPS.

Receiver performance

The low level of Code Detection Efficiency (<40 %) prompted the question, why was decoding unsuccessful for about 60 % of transmissions that had a correct Sync value? A potential explanation could lie in interference from a high rate of signal collisions, despite all transmitters by design emitting signals at variable intervals to minimise collision risks. However, this explanation lacked support for two reasons. Firstly, the manufacturer's guidance indicates Rejection Coefficient would be high if collision rate was high (Vemco 2010). However, Rejection Coefficients in the present study were consistently low (Fig. 4c). Secondly, opportunities for signal collisions would be rare unless study turtles persistently aggregated in one area. The latter was contradicted by their diverse patterns of space use (Supplementary material Fig. S2).

More generally, low Code Detection Efficiency and intermittent extremes in Noise Quotient could be ascribed to multiple sources of signal disruption such as wind, waves, turbidity, signal echoes and underwater noise (Heupel et al. 2006). Our study site was characterised by wind and wave exposure (due to offshore location), turbidity (see above *Space use by study turtles*) and hard coral reef surfaces that could generate acoustic echoes. Sources of biological noise included fish and reef organisms while vessel traffic contributed anthropogenic noise. Insight into the relative importance of these factors might be gained by assessing variation in receiver performance in relation to time of day, wind strength, tidal height and vessel traffic. However, the intra-day performance of our receivers could not be evaluated because Events data provided only 24-h values. If feasible in future upgrades, an option to aggregate Events data at shorter intervals would represent a useful enhancement of the Vemco system.

The reef habitat of our study animals was not optimal for acoustic tracking, given multiple sources of signal disruption mentioned above, but natural sources of interference could not be controlled. Given that detection degrades with distance (Fig. 2), more frequent detection could be achieved by deploying a greater number of receivers with closer spacing provided site characteristics allow, for example space for placing receivers without damage to coral. However, costs and benefits of deploying more receivers or using different technology would be

case-specific. Despite relatively low performance metrics, we were satisfied with the abundance of location data that our receiver array provided for multiple turtles concurrently. In terms of temporal resolution, our median time between detections (<3 min) compared very favourably with satellite tracking of marine turtles, in which many studies have received fewer than four locations per day, the latter further reduced by discarding low quality locations (e.g. Hays et al. 2001; Godley et al. 2003; Hart et al. 2012).

The diminishing trend in daily detections over time (Fig. 4d) defied explanation. It ran contrary to the trend in weather conditions that might have conferred an enhancement in acoustic transmission from progressively decreasing winds and wave action (JH pers. obs.; Australian Bureau of Meteorology data for Low Isles showed weekly average wind speed reduced by 10 km/h over the study period). Bio-fouling, which can degrade signal transmission (Heupel et al. 2006), was not observed during any underwater sightings of turtles equipped with transmitters. Bio-fouling of receivers was avoided by their regular servicing. The possibility of transmitter efficiency decreasing over time could not be ruled out. However, it seemed unlikely over the study duration, given the manufacturer's estimate of 10-year transmitter life. This puzzling finding highlights the need for future research into temporal variation in the efficiency of ultrasonic signal detection, for example by long-duration deployment of test transmitters at fixed locations within an array.

Influence of time step value

Results of the time step comparison (Table 3) were consistent with intuitive expectations. A time step without detection occurred more often when analysis was based on short time steps, resulting in a greater proportion of 'missing' locations. Equally, longer time steps allowed greater numbers of detections to be recorded within the time step and greater opportunity for detection by multiple receiver-stations. The latter could be beneficial because locations derived from multiple receiver-stations could in principle offer better geographic resolution than those derived from single or few stations, albeit at the cost of reducing temporal resolution. The trade-off between geographic and temporal resolution was demonstrated by a diminishing displacement rate (Table 3) indicating detail of turtles' movement trajectories had been lost with longer Δt values. Lost detail could also account for the slight decrease in spatial areas of UD contours derived from longer Δt values, although the effect was small for UD contours because they incorporated the very numerous locations accumulated over the study duration.

Short Δt produced a high proportion of time steps without detection. However, since each 'missing' location

represented a very short time span, this was of little importance. Notably the actual time between detections (independent of Δt) was predominantly very short, median across all turtles <3 min (Table 2). At the same time, the potential for a long Δt value to enhance geographic resolution applied to only a small proportion of locations, for example with $\Delta t = 60$ min, only 24 % of locations were derived from 3 or more receiver-stations. In summary, there was no clear benefit to be gained by using longer or shorter time steps in the present study, and therefore, we retained the initial choice of $\Delta t = 30$ min. The trade-off between adopting shorter or longer Δt values may be resolved differently in other studies, taking into account different research objectives, site characteristics, array design and typical movement rates for the study species. Importantly, the selected Δt value needs to be reported so that subsequent comparisons between studies can take into account the differential influences on quantitative measures derived from locations inferred for diverse Δt values.

Implications for turtle conservation management

Green turtles in Queensland waters are understood to maintain long-term associations with particular foraging areas, based on recaptures of marked individuals (Limpus et al. 1992; Limpus and Chaloupka 1997). However, repeat encounters with marked animals were infrequent and widely separated in time, meaning that the continuity of presence or absence of marked individuals during intervening periods (typically years) could not be assessed by mark-recapture methods. In contrast, our data reveal that multiple individuals maintained continuous or near-continuous occupation of a small geographic area during the 100-day study period.

The combination of long-term fidelity to foraging sites (shown by mark-recapture studies) and continuity of occupation (shown by the present study) indicates that individual turtles could suffer long-term exposure to any anthropogenic risks at a particular site. Thus, the need for site-specific mitigation of risk is heightened. At the same time, public support for mitigation measures could be enhanced if people in the local area know turtles are not merely transient visitors and appreciate that 'their' resident turtles will benefit from long-term protection.

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