

DIEL MOVEMENTS AND ACTIVITY RANGES OF GREEN TURTLES (*CHELONIA MYDAS*) AT A TEMPERATE FORAGING AREA IN THE GULF OF CALIFORNIA, MEXICO

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Abstract.—We examined the daily movements and activity ranges of Green Turtles at Bahía de los Angeles, a neritic foraging area in the Gulf of California, Mexico. Six turtles, ranging from 50.9 to 82.5 cm in straight carapace length were tracked with radio and acoustic telemetry for 24-h periods. Diel vagility ranged from 4.26 km to 15.34 km (mean = 8.21 ± 1.61 km), with minimum travel speeds of 0.18–0.64 km h⁻¹. Short-term (24-h) activity ranges were from 70 ha to 1,252 ha (mean = 458 ± 202 ha). As the first study to establish diel vagility of green sea turtles in foraging areas of the Eastern Pacific Ocean, our data show that Green Turtles may traverse large distances over limited temporal durations while resident at coastal foraging areas and may visit multiple habitats. Conservation efforts aimed to reduce the illegal hunting and incidental fisheries bycatch of Green Turtles assembled at this coastal foraging area must therefore encompass the entire coastal ecosystem rather than simply target a few component habitats within the area.

Key Words.—*Chelonia mydas*; Cheloniidae; Green Turtle; Sea of Cortez; Reptilia; Testudines; wildlife telemetry, vagility

INTRODUCTION

The Green Turtle (*Chelonia mydas*; Fig. 1) is a threatened species that occurs in tropical and subtropical regions throughout the world's oceans. Like most sea turtles, Green Turtles are migratory and use a wide range of broadly separated localities and habitats during their lifetime (for review see Hirth 1997). Among the most important sites for Green Turtles are neritic habitats rich in seagrass and/or marine algae where they forage and grow until maturity (Musick and Limpus 1997). Although Green Turtles have been the focus of research and conservation efforts worldwide, few data are available on their movement patterns and habitat requirements in these areas (Bjorndal 1997).

Understanding the spatial requirements of Green Turtles in neritic foraging areas is fundamental to their conservation (Bjorndal 1997; Bury 2006). Knowledge of daily movements and activity patterns can help elucidate the frequency and timing of visitation to key foraging and resting sites, and thereby pinpoint critical habitats (Seminoff et al. 2002; Makowski et al. 2006). Information on the spatial biology can also reveal variability in

life history strategies among disparate subpopulations (Bolten 2003). Further, because Green Turtles spend a vast majority of their lives in coastal foraging and developmental habitats (Musick and Limpus 1997; Plotkin 2003), where susceptibility to human impacts is high (e.g., Groombridge and Luxmoore 1989; Campbell 2005), understanding their movement patterns in these areas is a priority for ongoing conservation efforts. This information can guide decisions regarding the protection of foraging subpopulations, particularly in the Gulf of California, that continue to be impacted by illegal hunting and incidental bycatch (Gardner and Nichols 2003; Seminoff et al. 2003).

Two fundamental aspects of the biology of Green Turtles resident to neritic habitats are their diel vagility and diel activity range, respectively defined as a measure of the distance traveled by a turtle over the course of one 24-h interval, and the area traversed by a turtle over a 24-h period (Mendonça 1983; White and Garrott 1990). Because sea turtles spend 99% of their lives underwater, defining both of these components requires remote telemetry or in-water capture programs that are both labor intensive and expensive. Few investigations of diel movements in nearshore foraging areas have been undertaken as a result.

In this study, we used radio and acoustic (ultrasonic) telemetry to track six Green Turtles at a temperate foraging area in the Gulf of California, Mexico. The goal of this effort was to determine the diel vagility and diel activity ranges of Green Turtles. To our knowledge, this is the first study to determine the diel movement patterns of Green Turtles at a coastal foraging area in the Gulf of California. When combined with long-term telemetry and dietary studies in the area (e.g., Seminoff et al. 2002, 2006), we believe this information will provide an enhanced view of Green Turtle ecology in coastal foraging areas, thereby facilitating more effective conservation planning.

MATERIALS AND METHODS

Study site.—The study was conducted from August 1998 to July 1999 at Bahía de los Angeles (BLA; 28°58' N, 113°33' W), a NNE-oriented bay along the eastern coast of the Baja California Peninsula, México. A series of 17 islands line the north-eastern



FIGURE 1. A Green Turtle (locally known as a Black Turtle, *La Tortuga Prieta*) swimming in the Gulf of California, Mexico. Notice the Turtle Barnacles (*Chelonibia testudinaria*) adhered to this individual's carapace. Photographed by Martin Pepper.

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portion of BLA and separate this feeding area from pelagic offshore waters of the central Gulf of California. Bahía de los Angeles is ca. 60 km² in area, and characterized by strong tidal mixing and upwelling, which support productive marine benthic communities dominated by marine algae. Habitat characteristics of BLA are further described in Seminoff (2000). A small town also named Bahía de los Angeles is located along the western shores of BLA. The local economy for this community of ca. 800 persons is based on artisanal fisheries, sport fishing, and nature tourism. Ecotourism has expanded dramatically in BLA since 2000, but sea turtles, because of their low abundance, are still not among the focal species for visiting wildlife watchers.

Turtle capture and size.—As part of an ongoing study of Green Turtle demography (Seminoff et al. 2003), the six turtles examined in this study were captured with entanglement nets (100 m x 8 m, mesh size = 50 cm stretched) placed along the shallow perimeter (<10 m water depth) of the study area. Straight-line carapace length (SCL; ± 0.1 cm) and body mass (± 1 kg) ranged from 50.9 cm to 82.5 cm (mean 69.8 ± 4.5 cm) and 17 kg to 70 kg (52.3 ± 8.7 kg), respectively. Sex of turtles was undetermined for all but one turtle that was identified as a male (CM1) based on the presence of a differentiated tail (Wibbels 1999).

Tracking.—Green Turtles were instrumented with a very high frequency (VHF) radio transmitter (MOD 400, Telonics Inc., Mesa, Arizona, USA) and an acoustic (ultrasonic) transmitter (V16, VEMCO Ltd., Nova Scotia, Canada; or DT96, Sonotronics, Tucson, Arizona, USA). We attached VHF transmitters to the crown of the carapace using fiberglass cloth and resin (Balazs et al. 1996). The anterior and posterior ends of VHF transmitters were fit with fairings made with 10-minute quick-set putty to reduce hydrodynamic drag. Sonic transmitters were affixed to the carapace posterior with electrician ‘tie-wraps’ fit through two 3-mm diameter holes drilled in the marginal scutes (Renaud et al. 1995). Location of transmitters did not interfere with flipper movements. Weight of transmitter packages ranged from 250–400 g (0.4–1.5% of turtle body mass). Radio transmission frequencies ranged from 148.00 to 148.99 MHz, and acoustic transmissions were from 28.0 to 55.0 kHz; both frequency ranges are outside the hearing capacity of Green Turtles (30 Hz–1kHz, Ridgeway et al. 1969).

Instrumented turtles were released at their initial capture site

TABLE 1. Summary of size, sex, and tracking duration for each of six Green Turtles tracked in Bahía de los Angeles. SCL = straight carapace length; U = turtles of undetermined sex; M = apparent male based on presence of a differentiated tail.

Turtle ID	SCL (cm)	Weight (kg)	Sex	Relocation Interval				Total hours
				Begin		End		
				Date	Time	Date	Time	
CM1	77.5	70	M	08/29/98	2105	08/30/99	2114	24.15
CM2	65.2	41	U	08/28/98	1550	08/29/98	1700	25.17
CM3	71.4	50	U	08/15/98	2225	08/16/98	1959	22.43
CM4	82.5	75	U	08/16/99	1139	08/17/99	1235	24.93
CM5	50.9	17	U	08/05/99	0901	08/06/99	0906	24.00
CM6	71.3	61	U	08/30/99	1153	08/31/99	1233	24.66

within 24 h of capture, and tracked as part of long-term home range study (Seminoff et al. 2002). From 16 d to 65 d after the release of each turtle, we commenced continuous tracking efforts for one 24-h interval. We attempted to record a minimum of one resighting position each hour using a VHF receiver (TR-4, Telonics Inc., Mesa, Arizona, USA) with a 3-element Yagi antenna to track VHF transmissions, and a sonic receiver (VR60, VEMCO Ltd., Nova Scotia, Canada) with directional hydrophone to monitor acoustic transmissions. A 3.7 m inflatable boat (Achilles, Seattle, Washington, USA) with 25-horsepower outboard motor was used for all tracking efforts. To minimize disturbance to the turtles, each resighting coordinate was determined by maneuvering the tracking vessel to within 10–20 m of the turtle and recording the location of the tracking vessel with a Global Positioning System (Garmin [Europe] Ltd., Hampshire, United Kingdom; error range = ± 3 m to ± 12 m). Distances from telemetered turtles were determined through direct observation of surfacing turtles or estimated from the strength of the sonic signal at one-tenth gain with a directional hydrophone.

Statistical analysis.—Diel vagility was determined by calculating the distances (km) between successive resighting coordinates for one 24-h interval. To examine variability in movements throughout the diel cycle, we partitioned each track into diurnal (0500–1859 h) and nocturnal (1900–0459 h) periods. Vagility calculations assumed that Green Turtles followed a straight line between successive resighting locations, and should therefore be considered minimum estimates (Tremblay et al. 2006). Using the same set of resighting coordinates, we calculated short-term (24-h) activity ranges using the 100% Minimum

TABLE 2. Summary of diel vagility of six Green Turtles tracked by radio and ultrasonic telemetry in Bahía de los Angeles. Distances are summarized by day (0500–1859 h) and night (1900–0459 h) periods of activity. Diel (24-h) Activity Polygons were calculated with the MCP method (Burt 1943), % MCP is calculated as the ratio of the Diel Activity Polygon area and the summer MCP home range area reported in Seminoff et al. (2002a).

Turtle ID	No. Resightings	Distance Moved (km)			Minimum Travel Speed (km h ⁻¹)			Diel Activity Polygon	
		Day	Night	Total*	Day	Night	Overall	Area (ha)	% MCP area
CM1	28	11.91	3.43*	15.34	0.85	0.34	0.64	1 252	52
CM2	28	1.73*	2.52	4.26	0.12	0.25	0.18	257	33
CM3	20	4.49	3.08*	7.57	0.32	0.31	0.32	902	32
CM4	40	3.04*	3.35	6.39	0.22	0.33	0.27	70	10
CM5	40	2.86*	3.08	5.94	0.20	0.31	0.25	103	18
CM6	43	8.90*	0.86	9.77	0.64	0.09	0.41	165	17
Mean values:		5.49 ± 1.64	2.72 ± 0.39	8.21 ± 1.61	0.39 ± 0.12	0.27 ± 0.04	0.34 ± 0.07	458.2 ± 202.5	29.0 ± 7.2

*Adjusted for actual proportion of the 14-h day or 10-h night interval of tracking efforts (see Table 1). Calculations are based on constant velocity using the following equation: Corrected Distance = (24 / Tracked Interval (h)) * Total Track Distance

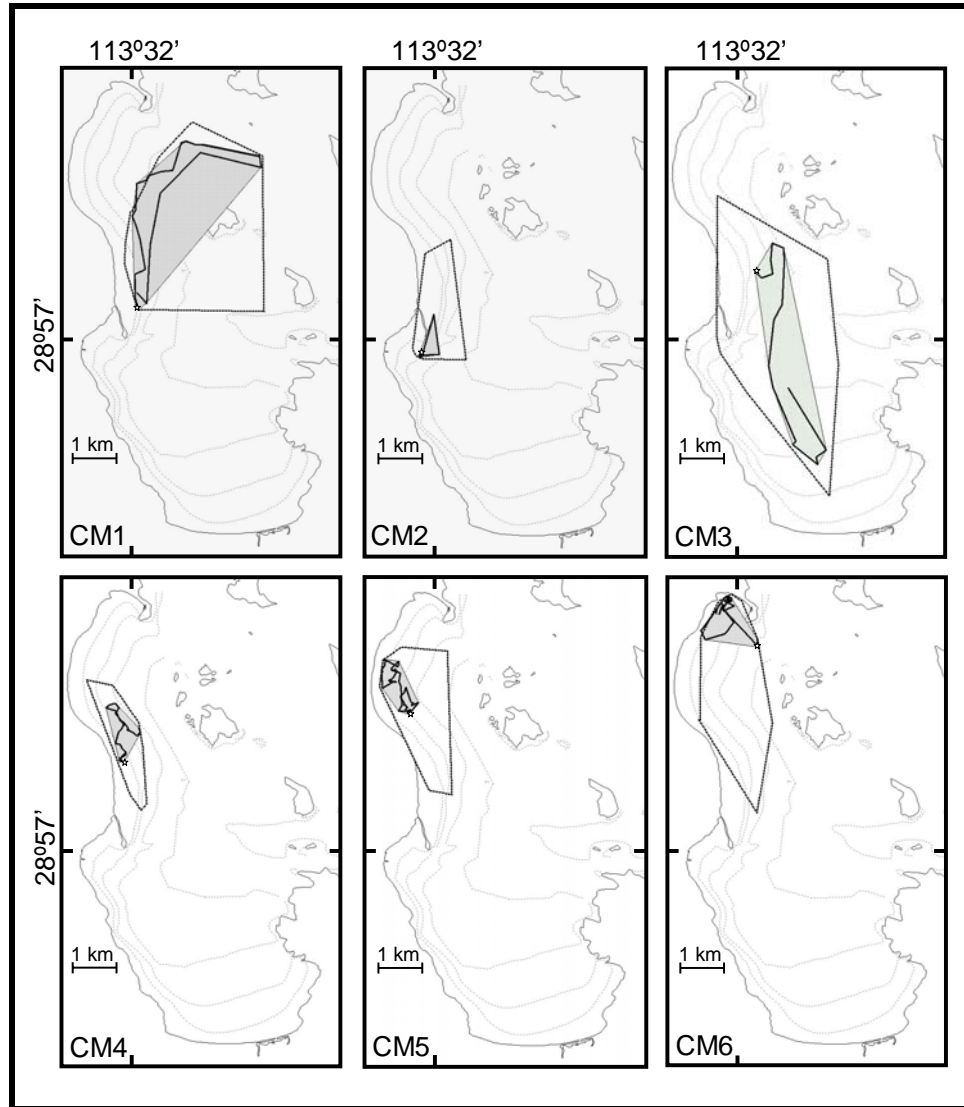


FIGURE 2. Diel vagility and activity polygons for six Green Turtles (*Chelonia mydas*) tracked in Bahia de los Angeles, Mexico. Solid black lines denote vagility; shaded areas represent activity ranges; hatched outer line reflects Minimum Convex Polygon home range area from Seminoff et al. (2002). Hatched lines indicate 10-m bathymetric contours.

Convex Polygon (MCP) method (Burt 1943) calculated with the Animal Movement Analyst Extension (Hooge and Eichenlaub 2000) in ArcView 3.2 geographic information system (GIS) software (Environmental Research Systems Institute, Redlands, California, USA). To model the effect of the size covariate and the tracking year factor on diel vagility and 24-h activity ranges, we used Generalized Linear Modeling (GLM; Cohen and Cohen 1983). Paired t-tests ($\alpha = 0.05$) were used to detect differences in diurnal versus nocturnal vagility and travel speeds. Statistical analyses were carried out with JMP software (SAS 1996). Mean values are followed by standard error (± 1 SE).

RESULTS

The 24-h tracking cycles were initiated during diurnal periods (0500–1859 h) for turtles CM-2, CM-4, CM-5, and CM-6; and during nocturnal periods (1900–0459 h) for CM-1 and CM-3

(Table 1). Resighting coordinates were gathered at least once per hour for all turtles except CM3, for which tracking efforts ceased after 22.44 h due to inclement weather.

Turtles were grouped into four categories based on horizontal movements (Figure 2): (1) those that remained within 3 km of the peninsular coast, in waters ≤ 30 m deep; (2) those whose movements were restricted to mid-bay waters between depths of 20 m and 50 m; (3) those that moved between peninsular shallow regions and mid-bay waters ≥ 30 m deep, but did not visit insular habitats; and (4) those that moved among shallow peninsular waters, mid-bay waters, and offshore insular habitats. Among these movement patterns, diel vagility ranged from 4.26 km to 15.34 km (mean = 8.21 ± 1.61 km; Table 2). The resultant minimum hourly travel speeds ranged from 0.18 km h^{-1} to 0.64 km h^{-1} (Table 2). In general, Green Turtles moved throughout the diel cycle, although greater distances were covered during diurnal periods (mean = 5.49 ± 1.64 km, range = 1.73–11.91 km) versus

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nocturnal periods (mean = 2.72 ± 0.39 km, range = 0.86–3.43 km; Table 1). This disparity in diurnal versus nocturnal movements was particularly evident in turtles CM-1 and CM-6 that covered 78% and 91% of their 24-h tracks, respectively, during diurnal periods. Despite this variation, there was no significant difference in distances moved between diurnal versus nocturnal periods ($t = 1.70$, $df = 1$, $P = 0.12$). The GLM model indicated that diel vagility was independent of tracking year and straight carapace length ($r^2 = 0.82$, $P = 0.48$). When inspected separately, there is no evidence that these explanatory variables significantly affected diel vagility (Table 2).

There was substantial variation in diel activity range size and shape among the six Green Turtles tracked during this study (Figure 2). Diel activity ranges were from 70 ha to 1252 ha (mean = 458 ± 202 ha). In general, these ranges were smallest among turtles whose movements were restricted to near-shore localities and were the largest for turtles that inhabited mid-bay waters exclusively, or visited insular sites. Diel activity polygons (DAPs) covered 10% to 52% (mean = 29 ± 7%) of each turtles' respective long-term MCP home range polygon (see Seminoff et al. 2002; Table 2), and were strongly correlated with the MCP area for each respective turtle (regression equation: $MCP = 1.6989DAP + 649.62$; $r^2 = 0.90$, $P = 0.0003$). This relationship suggests that turtles with larger overall home ranges also tended to move greater distances on a daily basis.

DISCUSSION

This study complements a previous home range study by Seminoff et al. (2002) that tracked the long-term home ranges of all six Green Turtles examined here. Whereas we included 20 to 43 resighting positions per turtle for developing the 24-hr tracks and activity ranges, Seminoff et al. (2002) determined the turtles' long-term home range sizes using 18 to 61 resighting positions, with ≤ 6 positions from any one 24-h period. With a maximum of 6 resighting coordinates from the present study also used by Seminoff et al. (2002), there is a low likelihood that their multiple use led to the significant size correlation between long-term home ranges and the diel activity ranges described here. This is supported by the shapes of the long-term MCP home ranges and 24-h activity ranges that are substantially different for each respective turtle (see Fig. 2).

The movements of Green Turtles in Bahía de los Angeles highlight the importance of this region as critical feeding habitat. The marine algal pastures along the shallow-water margins of the study area are epicenters of sea turtle activity, but our data indicate that turtles also visit mid-bay and insular habitats. Although we are less certain of the activities engaged in by Green Turtles as they depart these nearshore marine algae pastures, the offshore, deeper water (> 20 m) portions of the study area may offer important food resources or may be important for resting behavior. Seminoff et al. (2006) has documented a number of deep water invertebrate prey in the diet of local Green Turtles suggesting that Green Turtles forage in offshore regions of Bahía de los Angeles. Although few data are available on resting activity by local Green Turtles, observations from other foraging areas support our offshore resting theory. Mendonça (1983) showed that Green Turtles exhibited predictable diel movement patterns with turtles feeding on grass flats in mid-morning and mid-afternoon and moving into deeper water during midday hours. Green Turtles in St. Croix actively feed during morning and afternoon hours and rest offshore during

mid-day periods (Ogden et al. 1983).

Although all turtles were initially captured near/in nearshore algae pastures, not all turtles appeared at these sites during our study. This discrepancy suggests that Green Turtle visitation schedules to these habitats may occur during a temporal window that is greater than one day. A Green Turtle may not visit all of its preferred foraging and/or resting sites each day; it may require multiple days to access all of these habitats. Indeed, of the turtles we tracked, only two demonstrated a full 'round trip' during the 24-h tracking session. Variability in daily movement patterns of Green Turtles is known from Florida (Mendonça 1983) and Hawaii (Brill et al. 1995). Here, turtles adhere to different habitat visitation schedules.

The daily vagility measurements presented here should be considered as indicators of movement scales rather than as estimators of the specific distances covered by turtles. Nevertheless, these data elucidate characteristic behaviors of Green Turtles in foraging areas, and when compared with data on migrating turtles, highlight the ability of Green Turtles to shift behavioral modes depending on the habitats occupied. Whereas we derived a mean diel travel distance of 8.2 km, daily travel distances for Green Turtles departing the Michoacán rookery averaged 23.3 km (Byles et al. 1995). Similarly, Nichols (2003) reported mean daily travel distances of 26.0 km for satellite-tracked Green Turtles departing foraging sites in the Gulf of California en route to the Michoacán rookery. The variability in daily travel distances between this and other studies supports the theory that the various life-history phases (e.g., open-water migration, coastal residency) elicit different swimming behaviors by Green Turtles.

Although the travel speeds of Green Turtles residing in Bahía de los Angeles are less than migrating individuals from the same region, the daily vagility of Green Turtles in this study (8.2 km) was substantially greater than Green Turtles from other foraging areas. For example, summer diel movements for Green Turtles in Florida range from 1.2 to 4.1 km (Mendonça 1983) and daily vagility is 0.9 to 4.9 km for Australian Green Turtles (Whiting and Miller 1998). Renaud et al. (1995) reported a maximum vagility of 1.2 km d⁻¹ for Green Turtles in Texas. This disparity in movement scales between Green Turtle populations is also reflected in the 24-h activity ranges of Green Turtles in Bahía de los Angeles. Whereas we found a mean of 458 ha for 24-h activity ranges, the mean size of short-term foraging ranges for six Australian Green Turtles reported by Whiting and Miller (1998)

TABLE 3. Summary of the GLM parameter estimates fitted to Green Turtle diel movements and 24-h activity ranges. The *t*-test significance level is 0.05; ns: not significant.

Parameter	Estimate	SE	t-ratio	Prob (t)
Diel vagility				
(constant)	-34.45	42.31	0.81	ns
Year	-0.55	4.02	-0.14	ns
Straight carapace length	-0.61	0.99	-0.61	ns
24-h Activity range				
(constant)	-480.37	6396.51	-0.08	ns
Year	-382.70	608.11	-0.63	ns
Straight carapace length	30.97	150.21	0.21	ns

was 315 ha. Renaud et al. (1995) reported home ranges of 22 to 311 ha for juvenile Green Turtles in south Texas. The apparent differences in vagility between this and other sites perhaps relates to patchy distribution of food and shelter resources Bahia de los Angeles. This area is characterized by steep shores and a lack of extensive shallow water habitats that host food resources (Bray and Robles 1991). As a result, food is patchily distributed and separated from insular resting sites by up to 4 km (Pacheco-Ruiz et al. 1999). Green Turtles may therefore need to swim greater distances as they move among disjunct food patches and resting sites.

Management implications.—In the present study, seasonal differences in home range could not be investigated as all turtles were only tracked during summer (August). However, based on the large distances traveled and the diversity of habitats visited daily by Green Turtles in Bahia de los Angeles, conservation efforts aimed to reduce the illegal hunting and incidental fisheries bycatch of this endangered marine species may require expansion to encompass the entire coastal ecosystem rather than a few component habitats within Bahia de los Angeles.

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