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Post-nesting migrations of green turtles (*Chelonia mydas*) at Wan-An Island, Penghu Archipelago, Taiwan

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Abstract During the summers of 1994 to 1997, eight green turtles (*Chelonia mydas*) nesting at Wan-An Island, PengHu Archipelago, Taiwan, were equipped with satellite-telemetry transmitters. Using the Argos-linked satellite system, the turtles' migration routes were tracked until the transmissions stopped. The turtles migrated widely on the continental shelf to the east of Mainland China. The migration distances ranged from 193 to 1909 km, and the migration speeds from 1.2 to 2.8 km h^{-1}. The turtles apparently utilize several coastal areas as temporal residential foraging sites, and their migrations consist of both trans-oceanic and coastal legs. The wide distribution of the foraging sites of the turtles comprising this rookery reflects the extent to which the green turtle migrates in northeast Asia; regional and international cooperation will therefore be needed to conserve this declining population.

Introduction

Green sea turtles are known to make long-distance migrations, travelling hundreds to thousands of kilometres between their nesting and foraging sites (Mortimer and Carr 1987; Liew et al. 1995; Papi et al. 1995). In some cases, the turtles manage to locate distant islands in the seemingly featureless ocean (Papi and Luschi 1996). Tagging and even helium balloons have been used to study the migrations of sea turtles (Carr 1967; Meylan 1982; Mortimer and Carr 1987; Craig 1994). However, because of high tag-loss rates and because, even at best, only release and recapture location are recorded, these methods provide but scanty information. Since the early 1980s, satellite telemetry has allowed us to study the long-distance migration behaviour of sea turtles, including migration routes and diving times (Stoneburner 1982; Timko and Kolz 1982; Byles and Keinath 1990; Balazs 1994; Balazs et al. 1994; Renaud and Carpenter 1994; Liew et al. 1995; Papi et al. 1995), of both adults and juveniles (Bolten et al. 1994; Plotkin et al. 1994; Renaud 1994).

Wan-An Island, in the PengHu Archipelago, is one of the few remaining green sea-turtle nesting sites in Taiwan. The Council of Agriculture designated the nesting beaches as a sanctuary site in December 1995 (Cheng 1995; Council of Agriculture 1995). Nesting ecology has also been studied extensively (Chen and Cheng 1995). However, little is known about the whereabouts of the nesting turtles while they are at sea. This study, therefore, used satellite telemetry to determine the post-nesting migration routes and resident foraging area of nesting green turtles of the Wan-An Island colony.

Materials and methods

Seven adult *Chelonia mydas* were equipped with Argos-linked satellite transmitters (Telonics; Mesa, Arizona, USA) during the nesting seasons of 1994 through 1996. Three PTTs (platform terminal transmitter) were used, (ST-6, ST-3, and ST-14). The PTT ST-6 model is smaller than the ST-3 and operates over a shorter lifetime. It was used in 1994 because at that time we were not aware of its limitations. In 1995, a larger transmitter PTT ST-3, was employed, and from 1996 until 1997 another model, ST-14, analogous to ST-3. In 1997, the first turtle fitted with PTT ST-6 returned to Wan-An Island to nest. Although the PTT had been lost, she was identified by means of the Inconel tag on her right front flipper. We fitted her with a new PTT ST-14 in early August 1997.

After nesting or false crawling (crawling on beach with no nesting activity), turtles were captured before reaching the ocean and held in rectangular plywood pens in their natural prone position. Because of high humidity in the evening, PTT attachment was not carried out until the following morning. Attachment procedures followed those of Balazs et al. (1996). Briefly, Silicone Elastomer (Nephew and Nephew Rolyan Inc., Wisconsin, USA) was used to mould and mount the transmitter firmly against the carapace surface. The transmitter was then bonded to the carapace

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with fibreglass strips and surfboard (polyester) mixed-resin glue. The salt-water switches were covered with small pieces of masking tape before bonding to prevent accidental sealing of the switches. For convenience, all the tagged turtles were designated by the abbreviation of their nesting island (WA) followed by a number, a dash, and year of tagging. Body size, date of capture, and date of release of the eight green turtles are listed in Table 1.

The PTT repetition rate for three types of PTT was 50. The duty cycle (i.e. transmission programme) of the ST-3 and ST-14 were 3 h on/3 h off; the ST-6 PTTs were permanently switched on. Battery power was conserved both by the timing of the duty cycle and by the salt-water switch, which stops data transmission after 10 s submersion underwater. Although data on submersion times and water temperature were also transmitted, for the purpose of the present paper we were concerned only with the location of the turtles.

The transmitted data were received and processed by the Argos system (Taillade 1992). This system consisted of two NOAA Polar Orbiting Environmental Satellites (POES), which provide coverage of a ~5000 km-diam visibility circle on the earth's surface. The number of daily passovers increases with latitude, and can attain ~28 passovers per day at the North or South Poles (Argos 1996).

A "fix" is obtained each time a satellite receives and transmits. Based on a series of fixes, Argos then automatically calculates the location of the transmitter-turtle at levels of accuracy and confidence referred to as location classes (LC). Seven different location classes are used by Argos: Class 3 s, the most accurate location class, is calculated from at least four messages received during the satellite pass, and has an estimated accuracy of <150 m; Class 2 is relatively less accurate, and is calculated in the same way as Class 3, with an estimated accuracy range of $\geqq 150$ to <350 m; Class 1 is calculated in the same way as classes 3 and 2, with an estimated accuracy of $\geqq 350$ to <1000 m; Class 0 is calculated with an estimated accuracy of >1000 m; Class A receives three messages through Location Service Plus (auxiliary location processing in North America), with no estimated of location accuracy; Class B receives two messages through Location Service Plus, with no estimated of location accuracy; Class Z is the rejected location class, containing invalid locations (Argos 1996). To ensure a reasonable level of integrity for our data, only Location Class B or better, which provided a reasonable estimation of the migration path, were accepted; i.e. when positioning was near LC 1, 2, or 3 and the distance between the two points reasonably reflected the swimming speed of a turtle, and the location was not on land. Such positions were considered accurate and acceptable for the purposes of our study. The migration distance for each leg (i.e. distance between two locations) was calculated as a straight line between the two endpoints. Migration speed was calculated by dividing total migration distance (in km) on each trip by total migration period (h). Completion of a migration route was defined as when a tagged turtle stayed in the last location of the migration route for at least 7 d, or as the position at which the PTT battery ceased transmission.

Results

Individual migratory journies of *Chelonia mydas*

Turtle WA1-94

The magnetic bar was removed and the PTT ST-6 deployed at 06:30 h TST (Taiwan Standard Time) on 27 August 1994 on Wan-An Island (23°22′N; 119°30′E), PengHu Archipelago. This turtle left Wan-an Island on her post-nesting migration 2 d after tag deployment (Table 1). She arrived at Koshiki (31°46′N; 129°47′E), Japan, on 25 October 1994 (Fig. 1). The turtle travelled 190 km (1184 statute miles) at a calculated speed of 33.4 km d^{-1}, i.e. 1.39 km h^{-1} (Table 2). The last transmission and reliable position were from Koshiki on 28 October 1994 with the LC B (3 d after arrival). The total number of transmissions (all LC Zs included) was 208: 3% with LC 1, 16% with LC 0, 25% with LC A, 55% with LC B, and 1% with LC Z. The PTT transmitted 77 positions, with 5 instances of rejected data (6%).

Turtle WA2-94

The magnetic bar was removed and the PTT ST-6 deployed at 06:30 h TST on 28 August 1994 TST. The turtle left Wan-An Island for her post-nesting migration 17 d after tag deployment (Table 1). She arrived at a nearshore coral reef of coastal Taipei (25°13′N; 121°19′E), Taiwan, on 21 September 1994 (Fig. 2). The turtle travelled 323 km (201 statute miles) at a calculated speed of 46.14 km d^{-1}, i.e. 1.92 km h^{-1} (Table 2). The last transmission was on 27 March 1995 (187 d after arrival). However, the last reliable position was off the coast of Taipei on 16 March 1995 with the LC A (176 d after arrival). The total number of transmissions was 216: 3% with LC 1, 5% with LC 0, 18% with LC A, 69% with LC B, and 5% with LC Z. The PTT transmitted 83 positions, with 31 instances of rejected data (37%).

Table 1 *Chelonia mydas*. Date of capture, tagging, and release; and duration of tracks recorded by platform terminal transmitter (PTT) attached to green turtles nesting at Wan-An (WA) Island, PengHu Archipelago, Taiwan, between 1994 and 1997 (*CCL* curved carapace length; *SCL* straight carapace length)

	Turtle WA:							
	1-94	2-94	3-95	4-95	5-95	6-96	7-96	1-2-97
PTT	ST-6	ST-6	ST-3	ST-3	ST-3	ST-14	ST-14	ST-14
Body size (mm)								
CCL	96	111	94.5	99	106	97	100	99
SCL	93	106	92.5	92	101	91	97	97
Capture								
year	1994	1994	1995	1995	1995	1996	1996	1997
(day/month)	27/8	28/8	4/8	6/8	9/8	8/8	9/8	5/8
Tagged/released								
(day/month)	28/8	29/8	5/8	7/8	10/8	9/8	10/8	6/8
Track duration								
(d)	62	211	277	298	403	134	34	91

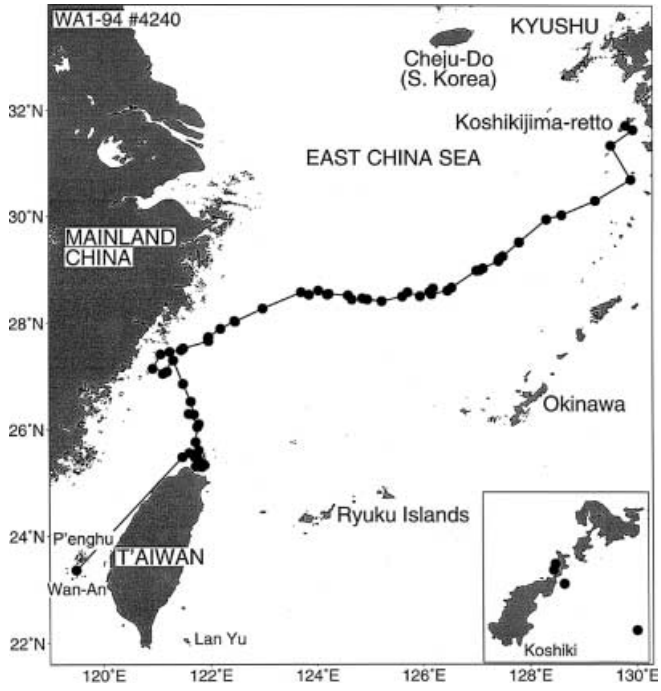

Fig. 1 *Chelonia mydas*. Track of Turtle WA1-94. Platform Terminal Transmitter (PTT) ST-6 was deployed on 27 August 1994; departure date of post-nesting migration was 29 August; estimated travel distance was 1904 km; arrival date at Koshiki, Japan was 25 October 1994

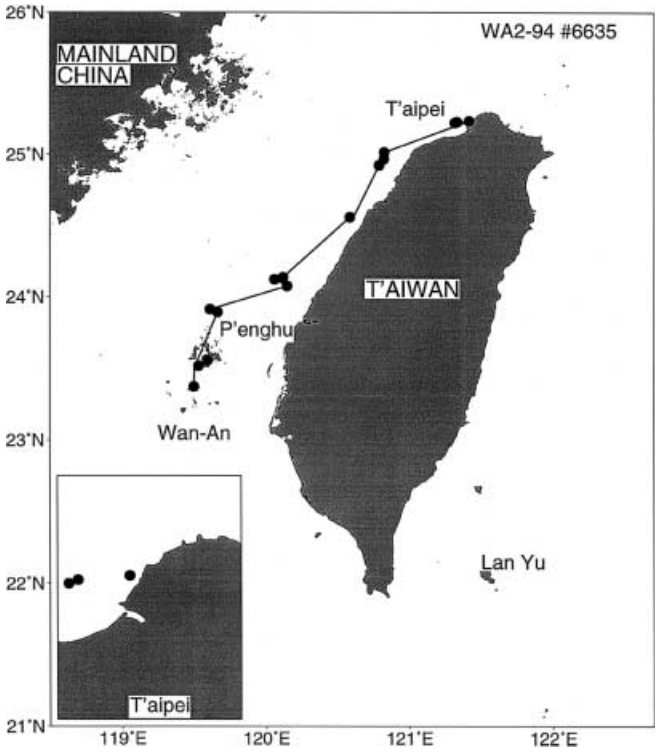

Fig. 2 *Chelonia mydas*. Track of Turtle WA2-94. PTT ST-6 deployed on 28 August 1994; departure date of post-nesting migration was 14 September; estimated travel distance was 323 km; arrival date at coastal Taipei, Taiwan, was 21 September 1994

Table 2 *Chelonia mydas*. Post-nesting migration distance, travelling duration, and swimming speed of green turtles nesting at Wan-An Island, PengHu Archipelago, Taiwan, between 1994 and 1997

Turtle Ref. No.	Distance (km)	Duration (d)	Speed (km h^{-1})
WA1-94	1904	57	1.39
WA2-94	323	7	1.92
WA3-95	1270	42	1.24
WA4-95	407	9	1.88
WA5-95	1130	17	2.77
WA6-95	1909	40	1.99
WA7-96	702	15	1.95
WA1-2-97	193	7	1.15

Turtle WA3-95

The magnetic bar was removed and the PTT ST-14 deployed at 06:00 h TST on 6 August 1995. The turtle left Wan-An Island for her post-nesting migration 2 d after tag deployment (Table 1). She arrived at a nearshore coral reef of the Hainan Dao (19°7′N; 110°37′E), Mainland China, on September 19, 1995 (Fig. 3). The turtle travelled 1270 km (790 statute miles) at a calculated speed of 30.24 km d^{-1}, i.e. 1.24 km h^{-1} (Table 2). The last transmission was on 10 May 1996 (233 d after arrival). However, the last reliable position was at Hainan Dao on 19 September 1995 with the LC A (3 d after arrival). The total number of transmissions was 231: 2% with LC 3, 3% with LC 2, 7% with LC 1, 6% with LC 0, 24% with LC A, 52% with LC B, and 6% with LC Z. The PTT transmitted 123 positions, with 33 instances of rejected data (27%).

Turtle WA4-95

The magnetic bar was removed and the PTT ST-14 deployed at 06:00 h TST on 7 August 1995. The turtle left Wan-An Island for her post-nesting migration 34 d after tag deployment (Table 1). She arrived at Qinpeng Dao (23°13′N; 117°16′E), Mainland China, on 18 September 1995 (Fig. 4). The turtle travelled 407 km (253 statute miles) at a calculated speed of 45.22 km d^{-1}, i.e. 1.88 km h^{-1} (Table 2). The last transmission was on 31 May 1996 (255 d after arrival). However, the last reliable position was at Qinpeng Dao on 30 January 1996 with the LC 1 (134 d after arrival). The total number of transmissions was 151: 7% with LC 3, 5% with LC 2, 9% with LC 1, 3% with LC 0, 18% with LC A, and 58% with LC B. The PTT transmitted 98 positions with 9 instances of rejected data (9%).

Turtle WA5-95

The magnetic bar was removed and the PTT ST-14 deployed at 06:00 h TST on 10 August 1995. The turtle left Wan-An Island for her post-nesting migration 49 d after

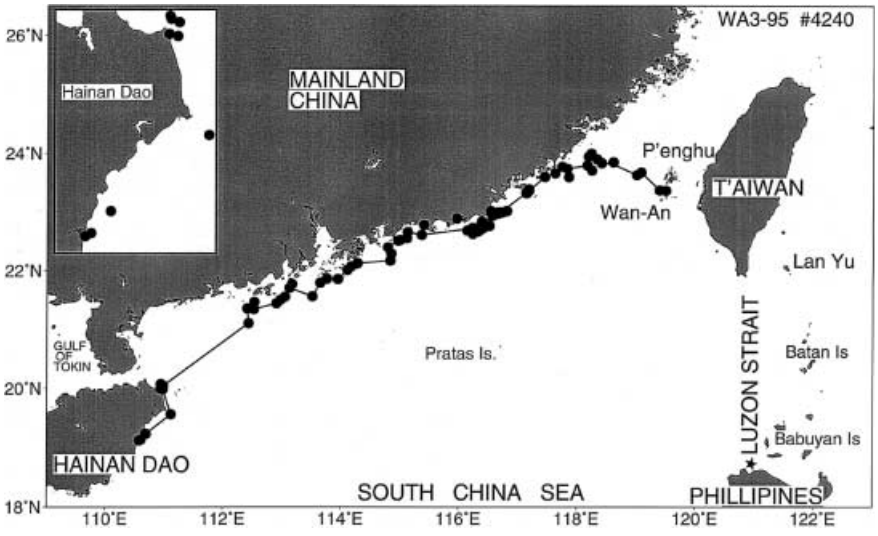

Fig. 3 *Chelonia mydas*. Track of Turtle WA3-95. PTT ST-14 deployed on 6 August 1995; departure date of post-nesting migration was 8 August; estimated travel distance was 1270 km; arrival date at Hainan Dao, Mainland China was on 19 September 1995 (*Star* site where Inconel-tagged turtle was caught in waters north of Philippines)

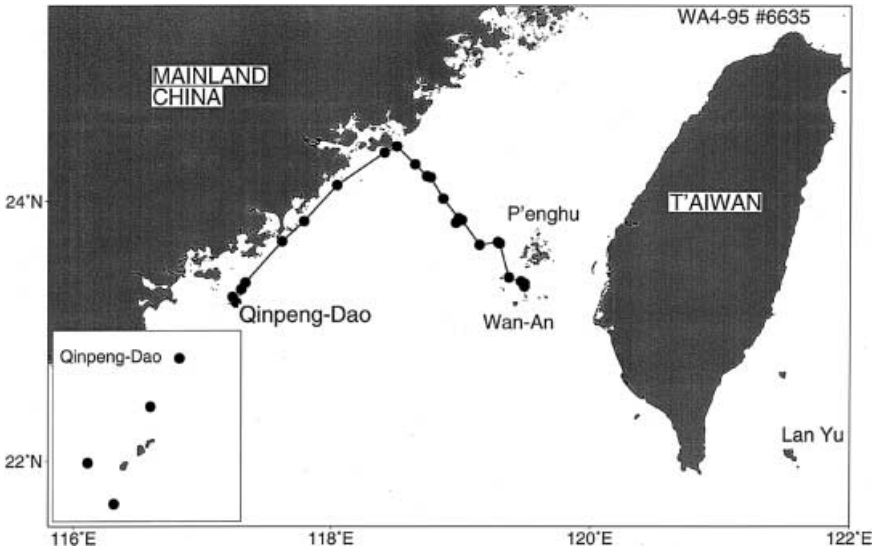

Fig. 4 *Chelonia mydas*. Track of Turtle WA4-95. PTT ST-14 deployed on 7 August 1995; departure date of post-nesting migration was 9 September; estimated travel distance was 407 km; arrival date at Qinpeng Dao, Mainland China, was 18 September 1995

tag deployment (Table 1). She arrived at Okinawa (26°31′N; 128°3′E) Japan on 15 October 1995 (Fig. 5). The turtle travelled 1130 km (702 statute miles) at a calculated speed of 66.47 km d^{-1} i.e. 2.77 km h^{-1}. The last transmission was on 18 September 1996 (337 d after arrival). However, the last reliable position was at Okinawa on 21 October 1996 with the LC B (6 d after arrival). The total number of transmissions was 240: 4% with LC 3, 5% with LC 2, 6% with LC 1, < 1% with LC 0, 25% with LC A, 58% with LC B, and 2% with LC Z. The PTT transmitted 123 positions, with 7 instances of rejected data (6%).

Turtle WA6-96

The magnetic bar was removed and the PTT ST-14 deployed at 06:30 h TST on 7 August 1996. The turtle left Wan-An Island for her post-nesting migration 67 d after tag deployment (Table 1). She arrived at Ishigaki-shima (24°38′N; 124°23′E), Ryukyu Archipelago, Japan, on 13 November 1996 (Fig. 6). The turtle travelled 1909 km (1186 statute miles) at a calculated speed of 47.73 km d^{-1}, i.e. 1.99 km h^{-1} (Table 2). The last transmission was on 19 December 1996 (27 d after arrival). However, the last reliable position was at Ishigaki-shima on 13 November 1996 with the LC 2 (0 d after arrival). The total number of transmissions was 188: 8% with LC 3, 4% with LC 2, 4% with LC 1, 1% with LC 0, 27% with LC A, 55% with LC B, 1% with LC Z. The PTT transmitted 93 positions with 13 instances of rejected data (14%).

Turtle WA7-96

The magnetic bar was removed and the PTT ST-14 deployed at 06:30 h TST on 9 August 1996. The turtle left Wan-An Island for her post-nesting migration 19 d after tag deployment (Table 1). She arrived at Dangan Liedao/Po Toi (22°5′N; 114°9′E), Mainland China, on 12 September 1996 (Fig. 7). The turtle travelled 702 km

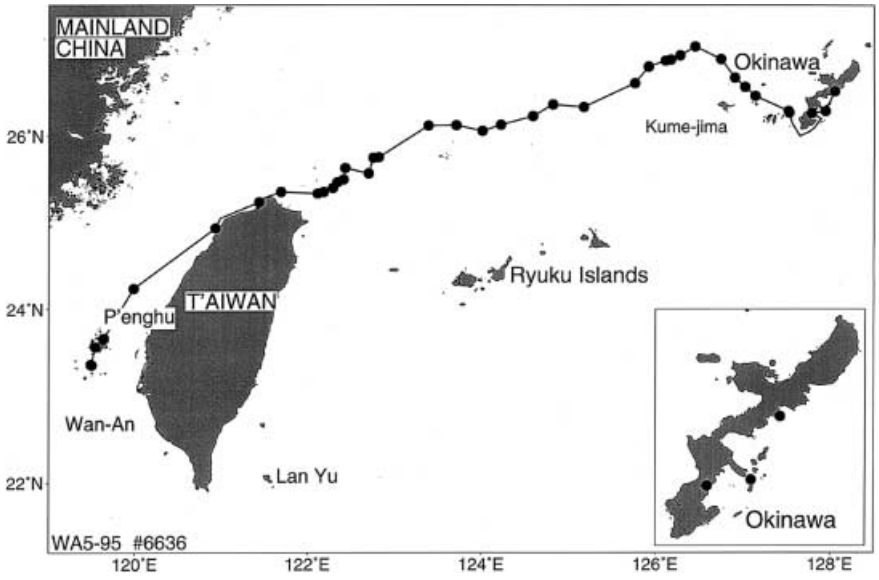

Fig. 5 *Chelonia mydas*. Track of Turtle WA5-95. PTT ST-14 was deployed on 9 August 1995; departure date of post-nesting migration was 28 September; estimated travel distance was 1130 km; arrival date at Okinawa, Japan was 15 October 1995

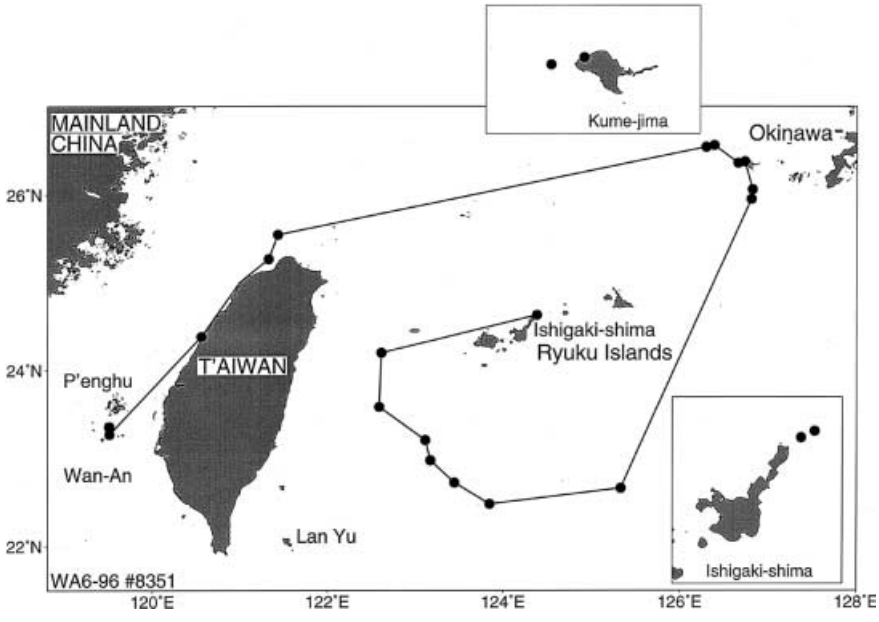

Fig. 6 *Chelonia mydas*. Track of Turtle WA6-96. PTT ST-14 deployed on 7 August 1996; departure date of post-nesting migration was 13 October; estimated travel distance was 1909 km; arrival date at Ishigaki-shima, Ryukyu, Japan, was 22 November 1996

(436 statute miles) at a calculated speed of 46.8 km d^{-1}, i.e. 1.95 km h^{-1} (Table 2). The last transmission and reliable position were at Dangan Liedao/Po Toi on 12 September 1996 (0 d after arrival). The total number of transmissions was 90: 3% with LC 3, 12% with LC 2, 2% with LC 1, 8% with LC 0, 21% with LC A, 51% with LC B, and 3% with LC Z. The PTT transmitted 61 positions with 3 instances of rejected data (5%).

Turtle WA1-2-97

The magnetic bar was removed and the PTT ST-14 deployed at 05:30 h TST on 7 August 1997. The turtle left Wan-An Island for her post-nesting migration 46 d after tag deployment (Table 1). The estimated departure date was 26 September. The PTT transit 7 d, and the turtle arrived at coastal Chunan County (24°40′N; 120°49′E), Taiwan on 3 October 1997 (Fig. 8). The turtle travelled 193 km (120 statute miles) at a calculated speed of 27.57 km d^{-1}, i.e. 1.15 km h^{-1} (Table 2). The last transmission was on 8 November 1997 (35 d after arrival). However, the last reliable position was on 31 October 1997 with the LC B (28 d after arrival). The total number of transmissions was 67: 11% with LC 3, 6% with LC 2, 6% with LC 0, 11% with LC A, and 72% with LC B. The PTT transmitted 19 positions with 6 instances of rejected data (32%).

Migratory patterns from 1994 to 1997

PTTs lasted from just >1 mo (34 d: Turtle WA7-96) to >13 mo (403 d: Turtle WA5-95) (Table 1). All but two

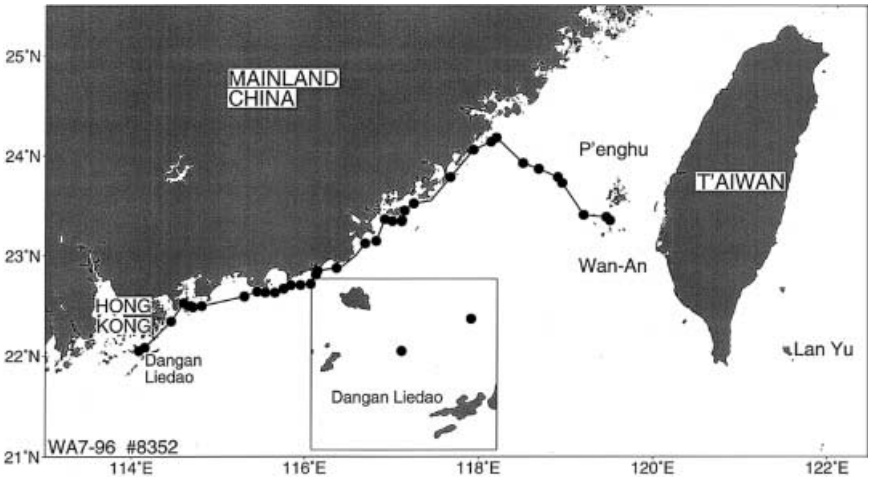

Fig. 7 *Chelonia mydas*. Track of Turtle WA7-96. PTT ST-14 deployed on 9 August 1996; departure date for of post-nesting migration was 28 August; estimated travel distance was 702 km; arrival date at Dangan Liedao/Po Toi, Mainland China was 12 September 1996

units (Turtle WA1-94 and Turtle WA7-96) operated for <3 mo, and provided enough information to reveal post-nesting migrations. The transmitter on Turtle WA1-94 transmitted for only 60 d, but still provided sufficient locations to enable the migration route to be tracked. However, we were not able to determine if the last location of this tracking was the turtle's permanent foraging site, because the PTT ceased transmission after the second day of her arrival. Turtle WA7-96 stopped transmission abruptly 15 d after nesting.

Five of the eight turtles migrated to the northeast, the others to the southwest of Wan-An Island. Migration distances ranged from 193 km (WA1-2-97) to 1904 km (WA1-94), and migration periods from 7 d (WA1-2-97) to 57 d (WA1-94). The turtles' estimated swimming speeds ranged from 1.15 km (WA1-2-94) to 2.77 km (WA5-95) per hour (Table 2). Migratory paths consisted of two stages. In the first stage, the turtles swam across the ocean from one nearshore zone to the other; in the second stage, they swam southward or northward along the coast.

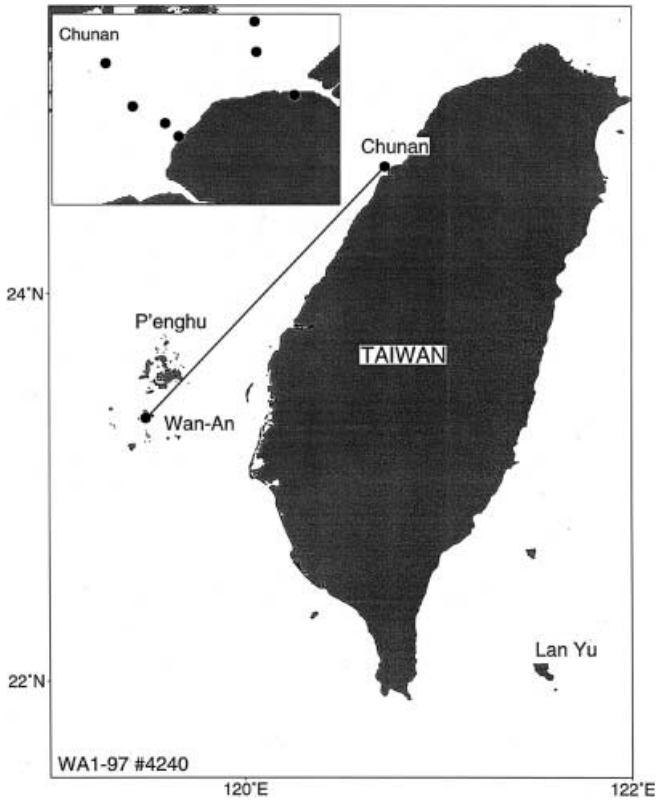

Fig. 8 *Chelonia mydas*. Track of Turtle WA1-2-97. PTT ST-14 deployed on 7 August 1997; departure date of post-nesting migration was 26 September; estimated travel distance was 1904 km; arrival date at coastal Chunan County, Taiwan was 3 October 1997

Discussion

Migratory behavior of the green turtle in Taiwan

Some sea turtles are known to make trans-oceanic migrations (Mortimer and Carr 1987; Bowen et al. 1995), while others migrate on local (e.g. Balazs 1994) or regional (e.g. Carr and Carr 1972; Papi et al. 1995) scales. The results of the present study on *Chelonia mydas* is the first to investigate post-nesting migrations of green turtles in northeast Asia, and our results suggest that they migrate from Wan-An Island to various locations on the continental shelf east of mainland China.

Migration speeds ranged from 1.15 to 2.77 km h^{-1} (mean value of 1.79 km h^{-1}: Table 2). These values are comparable to those found in other studies (Spring 1990; Balazs 1993; Keinath and Musick 1993; Balazs et al. 1994; Craig 1994; Papi et al. 1995).

We consider that the green turtles we tracked had two-stage migration patterns–oceanic and coastal. From their nesting sites, they migrated either to the northeast or to the southwest, i.e. swam across the Taiwan Straits (an oceanic leg) either towards Taiwan or mainland China, respectively; they then moved broadly northeast or southwest (a coastal leg) until they either reached their final destinations (e.g. WA2-94 and WA4-95), or

made another trans-oceanic migration (e.g. WA1-94, WA3-95, WA5-95, WA6-96).

All turtles except WA6-96 migrated entirely over the continental shelf. Nonetheless, the routes they followed were rarely the shortest distances between Wan-An Island and their final foraging ground (Fig. 1). They apparently preferred to migrate through coastal rather than oceanic waters, even when this involved detours that increased the overall migration distance. In term of fitness strategy, detours in an animal's migration path may result in excess energy expenditure and increased mortality risk (Sibly and Calow 1986). However, for animals undertaking long-distance migration with a low mortality risk as adults (Crouse et al. 1987; Heppell et al. 1996), and with infrequent breeding cycles such as the sea turtle, such constraints may not be as critical as other factors such as nesting- and foraging-site fidelity. Irrespective of how the turtles "remember" or "recognize" these routes (Luschi et al. 1996; Papi et al. 1997), the possibility of detour migration could be related to the fact that the turtles take advantage of the coastal waters as temporary foraging grounds in which they can "refuel" on their way to their permanent foraging sites.

Some turtles, such as WA2-94 and WA5-95 and even WA6-95, were able to pinpoint their target area after a long oceanic journey. How could the turtles recognize their final target areas with so many habitable coastal areas nearby? It is possible that isoclines and isodynamics of the magnetic field in the target area form a grid, allowing magnetic navigation of the green turtles (Lokmann 1992; Lokmann and Lokmann 1996). The same mechanism may also apply to a turtle that "refuels" in coastal waters, such as WA4-95 (who was also able to reach her target area after post-nesting migration).

One detour was inconsistent with this hypothesis: WA6-96 detoured into the Pacific near the Kume-jima, Ryukyu Archipelago, on 30 October 1996 for 14 d and then re-entered the East China Sea. Liu and Cheng (2000) found that during this part of her migration, this turtle changed her speed and direction under the influence of the Kuroshio current and impinging ocean eddies. Her migration speed over these 14 d ranged from 0.93 to 2.1 km h^{-1}, i.e. it did not differ from her speed at any other period of her post-nesting migration.

Since 1994, Turtle WA1-94 has returned to Wan-An Island to nest again – in 1997. However, her second migratory journey was not quite the same as her first (cf Figs. 1 and 7). Based on the study of Balazs (1983) and Limpus et al. (1992), Papi et al. (1995) suggested that green turtles have a high fidelity to both nesting and feeding grounds, and possess a two-way migration pattern. We did not observe this in the present study. WA1-94 migrated to coastal Chunan, Taiwan and stayed there for >1 mo in 1997 (in 1994 she migrated to Koshiki, Japan). This PTT stopped transmitting after 7 November 1997; thus we do not know if she continued to migrate northwards to Koshiki, Japan, after this date.

Although not formally part of this study, tag data from another turtle indicate that she also may have left the continental shelf. This turtle was tagged at the Wan-An nesting site with two Inconel tags (Tag No. TW064 on the right-front flipper and TW065 on the left-front flipper) in summer 1994. One month later she was caught by a fisherman in offshore waters north of the Philippines (location marked with star in Fig. 3), retagged by a conservation officer, and released. Unfortunately, her exact migration route could not be determined.

Genetic mtDNA analysis has shown that the turtles comprising the Wan-An rookery are distinct from those in other rookeries examined to date in the Pacific, including Japan, Hawaii, and Australia (P. Dutton personal communication). Several genetic and tag-return studies have shown the high fidelity of other green turtles towards their nesting and foraging grounds (Meylan 1982; Limpus et al. 1992; Allard et al. 1994; Bowen and Avis 1994). Thus, trips to the site from which the last transmitted data from each tagged turtle were should received clarify whether or not the putative end-points of the migrations of the turtles we studied do in fact constitute their adult foraging sites. Such "fact-finding trips" would also provide additional validation of the remote telemetry methods used in the present study.

Conservation implications

The present study has clearly demonstrated that green turtles nesting at Wan-An Island constitute an international resource. As they are dispersed throughout the waters of the Philippines, Japan, Taiwan, mainland China, and the Ryukyu Archipelago, conservation of the Wan-An rookery clearly cannot be the sole responsibility of PengHu County or indeed of Taiwan. Other satellite-tracking studies have also shown that turtles nesting in the same rookery disperse towards different feeding grounds (Balazs et al. 1994; Liew et al. 1995; Morreale et al. 1996). The widespread dispersal over the continental shelf also suggests that conservation of the marine habitat is at least as important as the nesting beaches themselves to the survival of sea turtle populations. Thus, a regional programme and strategy for long-term research on and the conservation of green turtles and their habitats are urgently needed to save this endangered species (IUCN 1995).

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