Zoological Studies **48**(1): 83-94 (2009)

Zoological Studies

Ten Years of Monitoring the Nesting Ecology of the Green Turtle, *Chelonia mydas*, on Lanyu (Orchid Island), Taiwan

I-Jiunn Cheng[1,*], Cheng-Ting Huang[2], Po-Yen Hung[1], Bo-Zong Ke[1], Chao-Wei Kuo[1], and Chia-Ling Fong[1]

[1] *Institute of Marine Biology, National Taiwan Ocean University, Keelung 202, Taiwan*

[2] *Department of Aquaculture, National Taiwan Ocean University, Keelung 202, Taiwan*

(Accepted May 15, 2008)

I-Jiunn Cheng, Cheng-Ting Huang, Po-Yen Hung, Bo-Zong Ke, Chao-Wei Kuo, and Chia-Ling Fong (2009) Ten years of monitoring the nesting ecology of the green turtle, *Chelonia mydas*, on Lanyu (Orchid I.), Taiwan. *Zoological Studies* **48**(1): 83-94. We report on the nesting ecology and environmental parameters of one of the largest green turtle, *Chelonia mydas*, rookery nesting site in Taiwan: Lanyu (Orchid I.), Taitung County, southeastern Taiwan. The site was studied from 1997 to 2006. Results showed that although turtles nest year-round, the main nesting season occurs in the warm and dry summer. Green turtles were forced to nest on the smallest beach, where anthropogenic disturbances were relatively low. The warm surface-water temperature tends to result in shorter inter-nesting intervals. Fewer nesters in poor nesting years were found to lay fewer clutches. The relatively wet and cooler weather and firm sand on Lanyu tends to increase the substratum compactness, resulting in relatively shallow nests. Larger females tended to deposit larger clutch sizes. Precipitation may be responsible for increased hatching mortality. The morphological characters of the hatchlings were found to be influenced by the egg characters. Although the population size of the study area is small, studies of the nesting ecology and conservation measures are still important to the regional population status, especially in the Asian region where most populations are either severely depleted and/or poorly understood. http://zoolstud.sinica.edu.tw/Journals/48.1/83.pdf

Key words: *Chelonia mydas*, Lanyu, Nesting ecology, Taiwan, Green turtle.

There is growing interest in providing objective assessments of both the regional and global status of sea turtle populations (Broderick et al. 2006), many of which are thought to be endangered to various degrees. To this end, the importance of publishing results from monitoring programs worldwide in peer-reviewed literature was identified (e.g., Seminoff and Shanker 2008). We thus set out to provide a comprehensive assessment of the status of green turtles, *Chelonia mydas*, at one of the largest rookeries in Taiwan.

Currently, only the green turtle is known to nest in Taiwan (Chen and Cheng 1995, Chen et al. 2007). Earlier investigations showed that major nesting sites are located on Wan-an I. in the Penghu Archipelago, Taiwan Strait and on Lanyu (Orchid I.) in Taitung County (Cheng and Chen 1994). Studies of the nesting ecology of green turtles on Wan-an I. have been carried out since 1992 (Chen and Cheng 1995), and the nesting beaches were designated as protected areas in 1995 (Cheng and Lin 1996, Cheng 2006). However, sea turtles in Taiwan still face threats from fisheries, marine pollution, direct harvests, egg poaching, sand mining, and other anthropogenic disturbances. There is a need to survey the major nesting sites in Taiwan in order to carry out effective sea turtle conservation measures.

---

[*] To whom correspondence and reprint requests should be addressed. Tel: 886-2-24622192 ext. 5303. Fax: 886-2-24648972. E-mail:b0107@mail.ntou.edu.tw

Based on results of field experiences from Wan-an and of pilot surveys from Lanyu in 1996, comprehensive monitoring was initiated in 1997 (Cheng 1998). These pilot studies suggested that more than 90% of nesting by green turtles occurs during the months of June to Oct., while occasional but unquantified nesting occurs throughout the rest of the year. Thus, we considered that data collected during the summer months would be valid for analyses of the nesting ecology of this population. The parameters collected in this study included sizes of both nesting females and hatchling turtles, remigration and inter-nesting intervals, nesting characteristics such as nest depth and clutch size, hatching statistics such as hatching mortality, and hatchling morphological characters. Environmental metrics, such as air temperature, precipitation, and sand particle characteristics of the nesting beach were also collected. This is the first long-term sea turtle nesting ecology study ever done in Taiwan. The purpose of this study was to determine the long-term trends of the nesting ecology traits of green turtles on this island to assist in evaluating the population status. Despite little being known about the in-water life-history traits of the green turtle near Taiwan, the nesting ecology parameters collected in this study also provide a suitable background for setting conservation priorities on Lanyu.

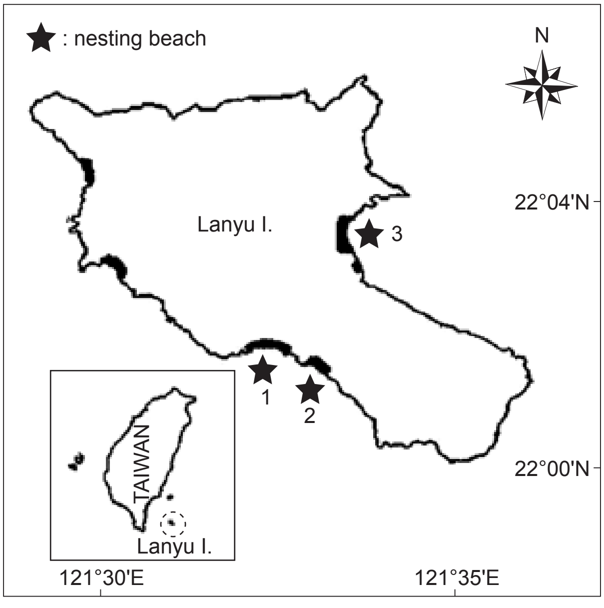

Fig. 1. Map of Lanyu, with nesting beaches denoted by stars. **1**, Big Badai beach; **2**, Badai beach; **3**, Donchin beach.

MATERIALS AND METHODS

Brief description of the study site

Lanyu (22°00'-22°08'N, 121°50'-121°60'E), Taitung County, Taiwan, is situated in the Pacific Ocean approximately 76 km off Taiwan's southeastern coast and has an area of about 45.7 km^2 (Fig. 1). Of the 6 beaches which exist on Lanyu, the pilot survey showed that the majority of nesting occurs on 3 beaches, (Badai, Big Badai, and Donchin beaches; Kuo 1999, Fig. 1). The respective lengths of these nesting beaches are 200, 1500, and 800 m for Badai, Big Badai and Donchin beaches. These beaches are dissipative, with less than a 5° slope, although the slope increases sharply (to > 20°) above the primary vegetation line. The vegetation on the beach is mainly composed of seashore vine morning glory (*Ipomocea pes-caprae* (L)), and screw pine (*Pandanus odoratissimus sinensis* (Warburg)).

Field surveys

Field surveys were carried out on foot from late June to early Sept. from 1997 through 2006. Two types of surveys were conducted: intensive nighttime surveys and morning track counts. Results from the pilot surveys showed that most turtles emerged to nest from shortly after sunset until 03:00 in the morning. Thus, during the nighttime surveys, nesting beaches were patrolled once every 2 h from 19:00 to 03:00 to count nesting events and to encounter nesting turtles. During periods with typhoons, which occurred mainly in Aug., the beaches were surveyed only during the daytime. During morning track counts, beaches were surveyed after daybreak for turtle tracks and to determine whether nesting had occurred. A nest was confirmed by direct observation, mainly at night, or the appearance of nest coverage towards the end of a set of tracks during the daytime. Emergence was recorded when a turtle first emerged from the water. Nesting success was defined as the proportion of emergences that resulted in a nest with a clutch of eggs.

The curved carapace length (CCL) and straight carapace length (SCL) of nesting turtles we encountered were measured (following the *MTSG manual* (Bolten 1999)), and each turtle was tagged on the trailing edge of the 2nd scale near the tail of the front and rear flippers using Inconel tags (National Band and Tag Co.) bearing unique characters; it was slated to be followed for 10 yr. Due to the high tag loss rate (Limpus 1992, Chaloupka and Musick 1997, Rivalan et al. 2005), PIT tags (Biomark Inc.) were also injected between the 2 largest scales of the left flipper or both hind flippers from 2002 onwards. The remigration interval was determined by tagged (Inconel tag) turtles that were observed nesting in more than 1 season. A new turtle was one that was untagged, while a remigrant turtle was one that had returned to a nesting beach after having been tagged the previous season (Miller 1997). The inter-nesting interval was defined as the time between when 1 nest was deposited and consecutive emergence dates within 1 nesting season by a tagged turtle (see the *MTSG manual*; Alvarado and Murphy 1999).

Nest data

Nests were protected against predation from red back pine root snakes (*Oligodon formosanus*) by setting up a plastic screen. Red back pine root snakes primarily feed on reptilian eggs (Coleman et al. 1993). They use an enlarged blade-like area of the maxillary teeth to slit the shell and insert their head into an egg and drink the contents (Toriba 1987). On Lanyu, they burrow into the beach sand and attack the nest (Hwang 1998). Occasionally, they were observed directly attacking a hatchling. All nests were dug out within 1 h after oviposition to install the screen. Each nest was surrounded by a plastic kitchen screen (with about a 1 mm mesh size), at least 10 cm away from the side of the clutch mass to avoid impeding the hatchling emergence behavior. Another round plastic screen was installed above the nest, 5 cm from the surface and sewed to the side screen to minimize the intrusion opportunity by snakes. The top screen was removed 5 d prior to the estimated hatchling emergence date (50 d; Cheng, unpubl. data) to avoid impeding hatchling emergence. Any nest susceptible to flooding was relocated. The nest depth and clutch size were determined before screen installation or nest relocation. Nest depth was determined with a fiberglass tape (± 0.1 cm) from the beach surface to the deepest position in the nest. Clutch sizes were determined by counting the eggs in each nest.

The incubation duration was determined as the date when eggs were deposited until the date when the 1st hatchling emerged on the sand surface of the nest. When the hatchlings emerged after midnight, 1 more day was added to the incubation duration. Hatchlings stay in the nest for 3-7 d prior to emerging onto the surface (Christens 1990). For logistic reasons and to avoid increasing the predation pressure from red back pine root snakes, we did not open the nest to determine the time when hatchlings emerged from the eggs.

The mean egg size and weight for each nest were determined by measuring 30 eggs. The egg size was determined by measuring the diameter of an egg with Vernier slide calipers (± 0.5 mm), and weight was measured with an electronic balance (± 0.01 g, Kang-Jen Model KH, Teipei). The total reproductive output (RO) was calculated as the product of the number of nests laid in a year and the mean clutch size (Mazaris et al. 2005).

Hatching data

Hatching success was calculated as the proportion of hatchlings among the total number of fertilized eggs. The number of fertilized eggs was determined by counting the remaining egg shells, hatchlings that remained in the nest, and appearance of signs of dead fetuses according to Miller (1985) in the eggs remaining in the nest. Post-hatching mortality was calculated as the proportion of hatchlings which died before emergence. Emergence success was calculated as the proportion of total hatchlings that emerged from the nest. Clutch survival was calculated as the product of hatching success and emergence success. Because both eggs and hatchlings are vulnerable to biotic and abiotic factors, the clutch survival rate was used to account for losses at the 1st stage of sea turtle life (Mazaris et al. 2005).

Because almost all of the nests were protected by screens, the nest was inspected every day after the top screen was removed. The nest was dug out 3 d after the emergence of hatchlings. The length and weight of the remaining hatchlings were measured. Hatchling length (SCL) was measured using Vernier slide calipers, and hatchlings were weighed using an electronic balance (Kang-Jen Model KH).

Environmental data

Sand grain characteristics

Sand samples were taken near the nesting sites at the same depth as the nest, and stored dry in double-sealed plastic bags. The beach sand characters were expressed as the mean grain size (graphic mean) and sorting (inclusive graphic standard deviation) (Folk 1974). The graphic mean (M_z; in mm) and inclusive graphic standard deviation (σ_1; unitless) were calculated according to Folk (1974):

$M_z (\O) = (\O_{16} + \O_{50} + \O_{84})/3$ and

$\sigma_1 = (\O_{95} - \O_5)/6.6 + (\O_{84} - \O_{16})/4$;

where, $\O_{16}$, $\O_{50}$, $\O_{84}$, $\O_{95}$, and $\O_5$ denote the respective proportions by weight of the total sand at 16%, 50%, 84%, 95%, and 5% of phi (Ø) value. Sand samples were collected in 1997-1998 and 2005-2006.

Climate data

Meteorological data collected for the study included average daily air temperature and precipitation on Lanyu from June to Oct. (1997-2006). Those data were purchased from the Central Weather Bureau of Taiwan (Central Weather Bureau, 1997-2006).

RESULTS

Field surveys

The main nesting season lasted from 15 June to 15 Sept., with the majority of nesting activities occurring from 1 July to 15 Aug. (Fig. 2). The nesting population ranged from 5 to 13 turtles per season (overall mean, 8 ± 3, Table 1, Fig. 3). As females are sometimes missed when they emerge to nest, the total nests laid each year was also included in figure 3. Results showed similar yearly trends between total gravid females and nests they laid. This suggests that the field survey carried out on Lanyu is a saturated method that covered all of the monitoring period.

Turtles emerged at annual means of 3-10 times each (overall mean, 7 ± 5, $n = 75$), and the mean number of nests deposited per individual annually was 1-4 (overall mean, 3 ± 2, $n = 75$). The overall mean value was defined as the mean value of all data throughout the study period, and the annual mean value was defined as the mean value of an individual year. The nesting success ranged 20%-60% (overall mean, 39% ± 31%, $n = 75$).

Among the 3 nesting beaches, more nesting occurred on Badai and Donchin beaches (one-way ANOVA, $F_{d.f.}$, $d.f. = 9$, $p < 0.001$). Eighty-four percent of nests were laid on Badai beach (overall mean, 20%), 14% (overall mean, 1.7%) on Donchin beach, and the remaining 2% (overall mean, 0.7%) nested on Big Badai beach.

The CCL of females varied 93-116 cm and SCL varied 86-111.3 cm with no differences among years (Table 1). There was a linear relationship between SCL and CCL (CCL = 18.527 + 0.828 SCL, $n = 68$, $r = 0.958$, $p < 0.001$).

The survey began in 1997, but the 1st remigrant turtle was not recorded until 2000. Based on conventional capture-recapture records (i.e., Inconel tags), the proportion of remigrant turtles since 2000 ranged 14%-64% (overall mean, 24 ± 21, $n = 10$, Table 1). The remigration interval

Table 1. Straight carapace length (SCL), curved carapace length (CCL), number of nesting females, and percentage of remigrant females on Lanyu from 1997 to 2006

Yr	SCL (cm) mean (S.E.)	CCL (cm) mean (S.E.)	number of female	% remigrant
1997	100.4 (6.4)	105.4 (5.7)	11	0
1998	95.0 (6.4)	100.5 (4.7)	5	0
1999	98.3 (2.7)	101.5 (3.9)	5	0
2000	99.4 (5.9)	103.4 (4.7)	5	40
2001	100.5 (6.0)	103.8 (5.4)	7	14
2002	102.9 (6.3)	106.75 (6.0)	3	31
2003	99.6 (6.4)	103.6 (6.2)	5	40
2004	96.5 (7.0)	101.4 (7.4)	5	20
2005	97.8 (5.7)	102.3 (3.7)	9	33
2006	99.0 (5.7)	104.4 (4.8)	11	64
Overall mean	99.5	103.9	8	24
S.E.	6	5.4	3	21

ranged 2-9 yr, with a mean value of 4.3 ± 1.8 yr (*n* = 20). Only 1 turtle among 20 cases returned to Lanyu for nesting activity in consecutive years. The mean interval between nestings ranged 9.7-12 d (overall mean, 10.6 ± 1.2, *n* = 163; Table 2), and significantly varied over the study period (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, *p* = 0.011).

Nest data

There was a positive, linear relationship between the number of nesters and the number of clutches each female laid (clutches/female = 5.766 + 2.984 (number of nesters), *n* = 10, *r* = 0.777, *p* = 0.008). The annual averages of nest depth ranged 57.7-73.1 cm (overall mean , 66.2 ± 11.7 cm, *n* = 197; Table 3). There was a significant difference among years in nest depth (one-way ANOVA $F_{d.f.}$, *d.f.* = 9, *p* < 0.001). Average clutch size ranged 73-110 eggs per nest (overall mean, 105 ± 28 eggs, *n* = 199). The clutch size was found to be positively related to the SCL of gravid females ((clutch size) = -122.661 + 2.265 (gravid female SCL), *n* = 10, *r* = 0.438, *p* = 0.025). The yearly means of incubation duration ranged 50-56 d (overall mean, 55 ± 4 d, *n* = 57; Table 4). Even though egg incubation extended from the summer to fall and even into the winter, the data were not broken up into monthly mean values. This is because the replicates were low, and most data were collected from late July to the 1st quarter of Sept. The data were not collected afterwards due to logistical limitations.

The yearly mean egg diameter ranged 37.6-43.7 mm (overall mean, 42.4 ± 2.8 mm, *n* = 7121), and the yearly mean egg weight ranged 40-47.6 g (overall mean, 43.3 ± 7.6 g, *n* = 7121). The total RO ranged 344 eggs/female in 1999 to 1430 eggs/female in 2002 (overall mean, 769 ± 381 eggs/female, *n* = 10).

Hatching data

The yearly mean hatching success ranged 53%-94% (overall mean, 80% ± 28%, *n* = 188). Annual mean post-hatching mortality ranged 0.1%-5%, and the yearly mean emergence success ranged 50%-93%, (overall mean, 79% ± 28%, *n* = 188). On a year-to-year basis, hatching mortality increased with the total precipitation during the nesting season (arcsin (hatching mortality/100) = 0.312 + 0.000148 (precipitation in mm), *n* = 10, *r* = 0.494, *p* = 0.023). Hatching mortality was also found to be influenced by egg size and weight (arcsin (hatching mortality/100) = -0.531 + 0.0238 (egg weight) + 0.0946 (egg diameter), *n* = 10, *r* = 0.599, *p* = 0.007). A forward stepwise regression analysis showed that egg diameter was the predominant factor (*p* = 0.031). The yearly mean clutch survival rate ranged 38%-85% (overall mean, 71% ± 33%, *n* = 188). An increasing trend of hatching success existed over the 10-yr study period (arcsin (hatching success/100) = -73.654 + 0.0373 (yr), *n* = 10, *r* = 0.684, *p* = 0.029). There was an increase of clutch survival throughout the 10 yr study period (arcsin (clutch survival rate/100) = -82.177 + 0.0365 (yr), *n* = 10, *r* = 0.724, *p* = 0.018).

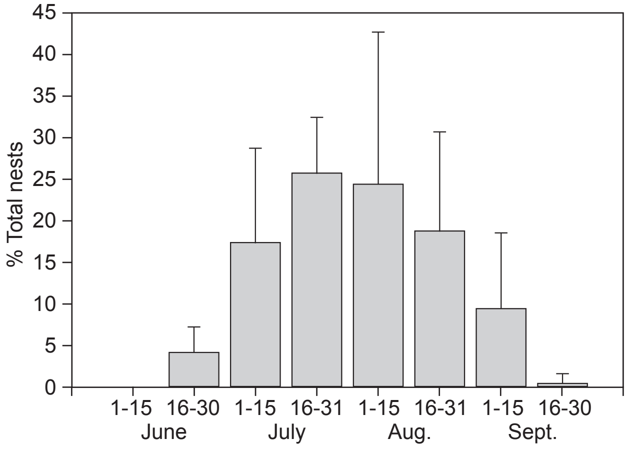

Fig. 2. Percentage of nests by month (with error bars denoting the standard deviation of the mean value) on Lanyu from 1997 to 2006. Major nesting activities occurred from 1 July to 15 Aug.

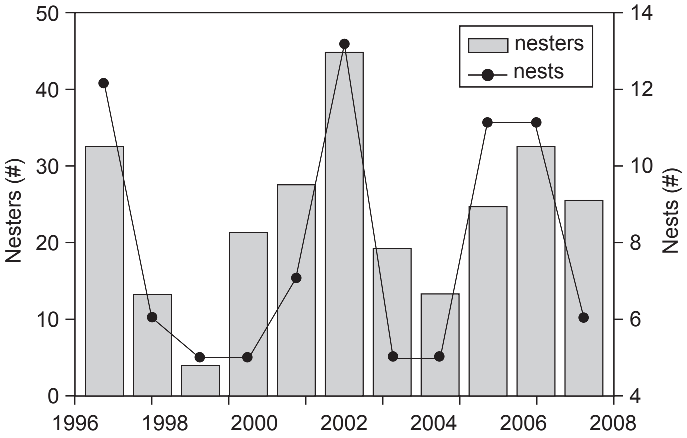

Fig. 3. Number of female green turtles nesting on Lanyu each year from 1997 to 2006.

The mean hatchling SCL ranged 43.9-47.7 mm (overall mean, 46.5 ± 2.1 mm, *n* = 1270). Mean hatchling CCL ranged 47.6-61.8 mm (overall mean, 46.5 ± 2.1 mm, *n* = 1176). Mean hatchling weight ranged 17.5-27.4 mg (overall mean, 22.1 ± 4 mg, *n* = 1239). The hatchlings were longest (SCL) in 2005 and 2006, and shortest in 2001 (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, $p < 0.001$), while their CCL was longest in 2000 (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, $p < 0.001$). Hatchling weight was greatest in 1998 and 2000 (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, $p < 0.001$). Hatchling SCL was positively related to both egg weight and egg diameter ((hatchling SCL) = 3.729 + 0.00468 (egg diameter) + 0.0195 (egg weight), $F_{d.f.}$, *d.f.* = 9, *r* = 0.52, regression analysis, *p* = 0.027). Hatchling weight also increased with egg weight ((hatchling weight) = -17.079 + 0.908 (egg weight), $F_{d.f.}$, *d.f.* = 9, *r* = 0.709, *p* = 0.022).

Table 2. Mean inter-nesting intervals (d) of green turtles on Lanyu from 1997 to 2006

Yr	Mean	S.E.	No. of replicates
1997	11.1	0.7	18
1998	10.5	1.4	12
1999	12.0	0	1
2000	11.2	1.4	14
2001	9.7	1.6	19
2002	10.8	1.2	29
2003	10.6	0.8	14
2004	10.7	1.0	9
2005	10.7	0.9	23
2006	10.1	1.0	24
Overall mean	10.6		

Environmental data

Nesting beach sand grain characteristics

The mean grain size (M_z) ranged from 0.37 (sand) to 3.21 mm (small pebbles), with an overall mean of 1.34 ± 0.79 mm (*n* = 256). The inclusive graphic standard deviation (σ_1) ranged 0.41-1.01 (indicating well sorted to poorly sorted, Folk 1974).

Climate data

The mean annual air temperature ranged from 22.5°C in 1997 and 2004 to 23.4°C in 1998 and fluctuated significantly among years (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, $p < 0.001$; Fig. 4). The total annual precipitation ranged from 2655.5 mm in 2005 to 43,414 mm in 1998, and was also high from 1997 to 1999 (Fig. 4). The wet years coincided with the El Niño event of 1998. The mean air temperature for the nesting season ranged from 24.9°C in 1997 to 25.7°C in 1998 and also fluctuated significantly among years (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, $p < 0.001$). Total precipitation for the nesting season ranged from 1172 mm in 2004 to 20,620 mm in 1998. The yearly precipitation also fluctuated significantly

Table 3. Nest depth (cm) on Lanyu from 1997 to 2006

Yr	Mean	S.E.	No. of replicates
1997	73.1	14.8	16
1998	61.7	7.5	10
1999	57.8	6.8	4
2000	57.7	8.1	21
2001	62.0	11.7	27
2002	69.3	11.2	43
2003	71.3	11.7	19
2004	59.4	13.4	5
2005	69.0	5.6	21
2006	66.6	12.1	31
Overall mean	66.2		
S.E.	11.7		
No. of replicates	197		

Table 4. Incubation duration (d) of green turtle nests on Lanyu from 1997 to 2006

Yr	Mean	S.E.	No. of replicates
1997	56	6.0	3
1998	50	2.1	2
1999	5	3.0	4
2000	56	4.8	8
2001	55	3.4	6
2002	5	2.5	6
2003	53	4.6	3
2004	52	3.0	7
2005	55	1.7	12
2006	55	4.2	6
Overall mean	55		
S.E.	4		
No. of replicates	57		

among years (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, *p* < 0.001). During the survey period, the temperature was highest in June and Aug. and lowest from Dec. to Mar. (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, *p*< 0.001). There was a significant monthly variation in precipitation (one-way ANOVA, $F_{d.f.}$, *d.f.* = 9, *p*< 0.001). The precipitation was highest in the month of Jan. and lowest from Mar. to Aug.

DISCUSSION

Nesting environment

It is well known that sea turtles exhibit nesting seasonality, both for those populations that nest at high latitudes where the summer is relatively short, as well as those populations nesting in the tropics (e.g., Godley et al. 2001, Antworth et al. 2006). This nesting seasonality is presumably a consequence of females timing their reproductive activity to coincide with conditions that are most conducive to maximizing reproductive fitness. Similarly, we found marked nesting seasonality with turtles on Lanyu which mainly nested in the dry, warm season on the island when the weather is relatively stable. Elsewhere, green turtles nest in the warm/wet part of the season, and this has been suggested to aid female excavation of nests (Mortimer and Carr 1987). A meta-analysis of different green turtle populations may help identify the most important drivers of nesting seasonality across different sites.

Hays and Sutherland (1991) suggested that beach fidelity allows the repeated use of a favorable nesting site. In this study, females nested mainly on Badai beach, the smallest nesting beach on the island, and showed the possibility of high nest site fidelity. However, we feel that this might not be the case in this study. Anthropogenic impacts, such as sand mining for house construction; littering from local villages; light pollution from households, coastal highways, and major hotels; and various night activities such as tourists walking on the beach, from beach sport fishing to hunting for coconut crabs, were high at the other 2 beaches, but they were relatively low at Baidai beach. That is because (1) it is small and relatively inaccessible to visitors and (2) it is located near a traditional cemetery. The native people on the island, the Yami, believe that to stay or pass by this beach will bring bad luck to their family. Thus, green turtles may be concentrated on Badai beach due to a lower level of disturbance. The mean grain size and inclusive graphic standard deviation were well within the range for nesting beaches for green turtles (i.e., fine sand to coral pebble; Mortimer 1995).

Life history traits of nesting green turtles

Morphological characteristics of female green turtles

The nesting population on Lanyu is rather small, and at the same time contains a substantial proportion of new recruits. The new recruits were distinguished from remigrants that had lost their

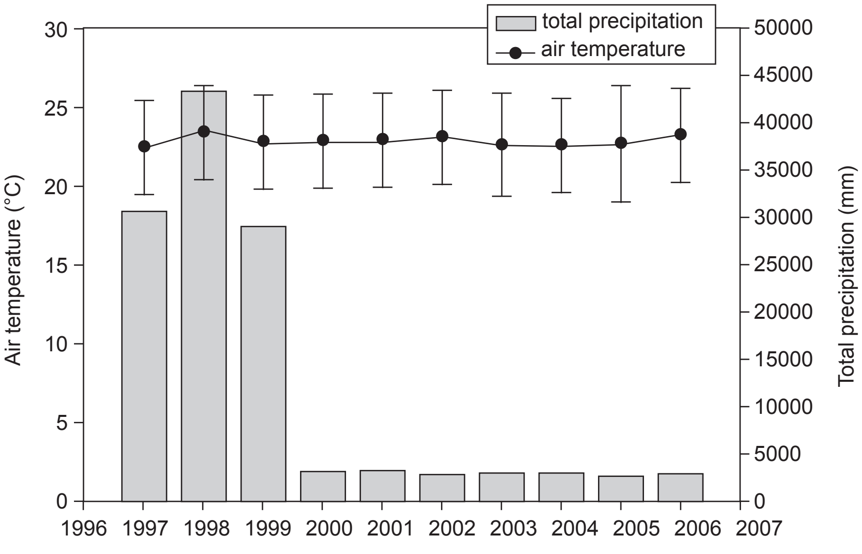

Fig. 4. Yearly total precipitation and mean air temperature on Lanyu from 1997 to 2006.

tags by 2 methods: the size difference, by which recruits were usually smaller (thus younger) than the remigrants; and the second is to check whether the flippers of untagged turtles had a "tag scar". If she had no scar, then the chance of being a recruit was high; otherwise she was assigned as a remigrant turtle. However, due to the high tag loss rate, the proportion of new recruits to the nesting population needs further evaluation. The application of the capture-mark-recapture (CMR) method with PIT tags can properly resolve this problem (Rivalan et al. 2006). In spite of the nesting population being small, this small population may still be very important in terms of regional conservation of the species (Broderick et al. 2002, Godfrey and Godley 2008), especially in the Asian region where most populations are severely depleted (e.g., Chen et al. 2007) and/or the current population status is poorly understood.

Nesting characteristics

The yearly means for the inter-nesting interval were short compared to those of other studies (Mortimer and Carr 1987, Eckert 1993, Sato et al. 1998, Hermann et al. 2000, Hays 2000, Broderick et al. 2001, Limpus et al. 2003). This difference in the inter-nesting interval was apparently due to differences in surface water temperature (SST) among the several nesting habitats during the oviductal phase of embryogenesis and shell formation (Miller 1985, Sato et al. 1998, Hays et al. 2002, Limpus et al. 2003). Elsewhere the Q_{10} for the water temperature effect on the inter-nesting interval was found to be high at > 3.0 (Sato et al. 1998). Measurement of SST near the nesting site was not possible logistically. However, due to the fact that Lanyu is located in the main stream of the warm Kuroshio Current, it is likely that the warm surface waters can result in short inter-nesting intervals.

The positive linear relationship between the number of nesters and clutches is consistent with data for green turtles nesting on Cyprus (Broderick et al. 2003), where fewer nesters breed in poor nesting years and also each nester lays fewer clutches. Thus, the variation in reproductive output might mainly be caused by fluctuations in ocean-climatic conditions that affect food availability (Limpus and Nicholls 1988).

The yearly nest depth means fell within the range of studies in Turkey (Özdemir and Türkozan 2006) but were shallower than those at Raine I., Australia (Limpus et al. 2003) and Ascension I. (Hays et al. 1993). The nest depth in our study site was also shallower than at the other nesting site in Taiwan on Wan-an I., Penghu (Cheng et al. 2008). There are 2 processes influencing nest depth. The 1st process is the depth of the body pit, with females generally removing the surface dry sand. Thus, drier sand may lead to a deeper body pit. The 2nd process is the depth of the egg chamber. Here it is most probably the size of the female that influences the depth of the egg chamber, since females reach down as far as possible with their rear flippers when excavating the bottom of the egg chamber. Thus, deep nests on Ascension I. are a consequence of (a) dry surface sand and (b) large females (Hays et al. 1993).

The difference in the nest depth between Wan-an and the study site might be related to the different nesting environments. The sand on Lanyu beaches is composed of quartz propyrite, occasionally inter-layered with muddy sediment (Natural Conservation Society ROC, 1988), while sand on Wan-an beach is composed mainly of quartz propyrite, coral, and shell debris (Chen and Cheng 1995). In addition, the nesting season on Wan-an I. is drier and hotter than on Lanyu (Cheng, unpubl. data). The character of the sand on Wan-an I. might result in low cohesiveness among particles. Thus, the dry front can penetrate deeper into the beach, and turtles have to dig deeper nests on Wan-an I. in order to successfully deposit their eggs. The relative wet and cooler weather and sand substratum characters on Lanyu would increase the substratum compactness and limit the depth to which the turtles could dig.

Hatching characteristics

Larger females tend to deposit larger clutches (McGinley 1989, Hays and Speakman 1991, Hays 2001). A similar result was found in the present study; with clutch size being positively related to the SCL of gravid females. The influence of precipitation on hatching success suggests that precipitation is the main source of water in the upper beach substrata, and is important for embryogenesis (Ackerman et al. 1981, Rattermen and Ackermann,1989). However, excess precipitation will impede the exchange of water vapor and oxygen between the eggs and their surroundings, causing embryo asphyxiation and increasing hatching mortality (Tracy et al. 1978, Kam 1994, Tucker et al. 1998, Foley et al. 2006). The effect of egg characters on hatching mortality suggests that larger eggs, especially with a greater egg surface area, will not only increase oxygen consumption by the nest but will also produce more cumulative metabolic heat during embryogenesis. Exchanges of gas and water vapor within the nest and between the nest and the surroundings are mainly mediated by diffusion (Ackerman 1997). The increase in oxygen consumption decreases oxygen availability within the nest. The increase in metabolic heat during the exponential growth phase also results in an outflow of water from the nest (Packard et al. 1985). Both factors might result in increased hatching mortality. In spite of this drawback, larger hatchlings crawling faster during the emergence phase enjoy higher emergence success (Bell et al. 2003, Gutzke et al. 1987, Packard et al. 1999).

Climate change is likely to impact sea turtles through a change in hatching sex ratios, since turtles exhibit temperature-dependent sex determination. Also, changes in air temperature can cause changes in incubation temperatures. Climate change might also lead to varying levels of precipitation. Increased precipitation will likely lower incubation temperatures and, as shown here, may also severely impact hatchling success (Houghton et al. 2007). These combined impacts of precipitation need to be considered when the overall impacts of climate change for sea turtles are assessed.

An increase in the hatching success was found throughout the 10 yr period (Fig. 5). Anthropogenic disturbances were high on the nesting beach, and interference with nesting activities was frequent when the project was initiated. In addition, nest predation by the pine root snakes was a major threat on the nesting beach. Intense beach patrols and improved screening techniques might have decreased the natural predation and human disturbances, and thus decreased egg mortality. Low post-hatching mortality resulted in hatchling emergence success which was quantitatively similar to hatching success. Another important contributing factor is the decrease in precipitation since 2000 (Fig. 4), which decreased hatching mortality.

Clutch survival represents 1 component of recruitment to the next generation (Mazaris et al. 2005) and has been found to be related to factors in the incubation environment, such as nest depth, variation in the water potential during embryogenesis, electrical conductivity in pore water, and pore space volume (Mortimer 1995). The large variation in clutch survival observed in this study thus might be related to small-scale variations among nesting environments. In spite of the increase in clutch survivorship over the 10 yr study period, the precipitation during the nesting season decreased from 17,005 mm in 1997 to 1282 mm in 2007, while air temperature varied little over the same period of time; hatching mortality was also found to decrease with decreasing precipitation. Thus, the nesting environment might have been improved by a decrease in conditions leading to asphyxia within the nest. This, in turn, improved the clutch survival rate by enhancing hatching success. However, the nest temperature can determine the hatchling sex ratio (Yntema and Mrosovsky 1982). The high precipitation will probably reduce the nest temperature and lead to more male hatchlings being produced (Houghton et al. 2007). Thus, the encouraging results of long-term increases in hatching success are also likely to be paralleled by a change in the hatchling sex ratio, towards more female hatchlings being produced.

Morphological characteristics of hatchlings

The influence on hatchling morphological characters (e.g., SCL, CCL, and weight) of the egg weight and diameter suggests that egg characteristics influence hatchling morphological characters. This result is consistent with findings of Glen et al. (2003) that differences in maternal effects and temperature result in differences in egg size, which in term contribute to differences in hatchling size between green turtle populations on Ascension I. and Cyprus.

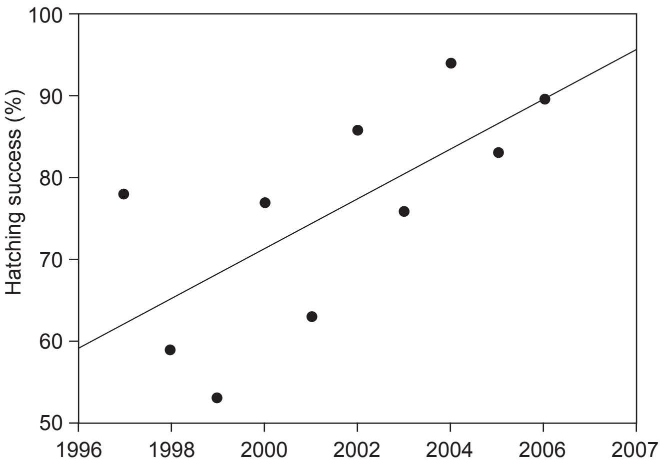

Fig. 5. Trends of increasing hatching success of green turtle nests on Lanyu from 1997 to 2006. Each dot denotes the yearly mean value.

In common with other studies at nesting sites, our work focused on female turtles. There is clearly a need to learn more about male turtles which have historically been hard to study since they do not come ashore to nest. Although difficult, the capture of male turtles is possible (e.g., Hays et al. 2001, James et al. 2005), and furthermore, it is possible to assess the number of male turtles from a DNA analysis of hatchlings (Lee et al. 2007). These sorts of studies are therefore important to gain a greater understanding of sea turtle breeding populations, especially given concerns that global warming might lead to a highly female-skewed sex ratio.

Conservation implications

Lanyu is one of the largest rookery nesting sites in Taiwan. However, the size of the main nesting beaches on the island has shrunk dramatically in recent years. Most of the nesting activities occurred on the smallest nesting beach: Badai beach. Both genetic analyses (Dutton, pers. comm.) and satellite telemetry (Cheng, unpubl. data) suggest that turtles frequenting this nesting rookery might use waters around Penghu as their foraging ground. Thus, nearshore fisheries may pose another threat to the pelagic life stages of green turtles. In addition, a genetic analysis showed that the haplotypic diversity of this population is 0 (Cheng et al. 2008). Furthermore, the construction of mercury streetlights along the coastal highway by the Badai beach in 2006 have brightened most of the nesting beach and forced gravid turtles to relocate their nests to a shaded area on the tourist-exposed beach, Big Badai beach, near a sewage outfall. Although Hays (2004) suggested that the Allee effect does not seem to occur in small sea turtle populations (e.g., Balazs and Chaloupka 2004), the combined stresses from both habitat destruction and genetic isolation have downgraded this local population to a critically endangered status. Thus, serious conservation measures are desperately needed, including the establishment of a protected area, light-pollution control, enhanced screening of nests to reduce snake predation, awareness campaigns, and restriction or termination of sand mining and other human activities on the nesting beaches to save this species from extirpation in the near future. Because most sea turtle populations in Asia are either severely depleted or their population statuses are poorly understood, the loss of this small but well-studied population would be a great loss to regional conservation efforts (e.g., Godfrey and Godley 2008).

Acknowledgments: The authors would like to thank Ms. W.L. Kuo, Mr. L.J. Jeng, Mr. K. Zong, several volunteers, and Coast Guard personnel for their field assistance. Critical and constructive comments from G.C. Hays and G.H. Balazs reviewer are deeply appreciated. All work was conducted in accordance with Taiwanese legislation (Council of Agriculture 2000-2006). This project was supported by grants made available to I.J. Cheng from the Taitung County government and Forestry Department, the Council of Agriculture, Taiwan from 1997 to 2006, and the I-Mei Environmental Protection Foundation.

REFERENCES

Ackerman RA. 1981. Growth and gas exchange of embryonic sea turtles (*Chelonia mydas*). Copeia **1981:** 757-765.

Ackermann RA. 1997. Chapter 4. The nest environment and the embryonic envelopment of sea turtles. *In* PL Lutz, JA Musick, eds. The biology of sea turtles. New York: CRC Press, pp. 83-106.

Alavarado J, TM Murphy. 1999. Nesting periodicity and internesting behavior. *In* KL Eckert, KA Bjorndal, FA Abreu-Grobois, M Donnelly, eds. Research and management techniques for the conservation of sea turtles. Washington DC: IUCN/SSC Marine Turtle Specialist Group Publication no. 4, pp. 115-118.

Antworth RL, DA Pike, JC Stiner. 2006. Nesting ecology, current status and conservation of sea turtles on an uninhabited beach in Florida, U.S.A. Conserv. Biol. **130:** 10-18.

Balazs GH, M Chaloupka. 2004. Thirty-year recovery trend in the one depleted Hawaiian green sea turtle stock. Biol. Conserv. **117:** 491-498.

Bell BA, JR Spotila, FV Paladino, RD Reina. 2003. Low reproductive success of leatherback turtle *Dermochelys coriacea*, is due to high embryonic mortality. Biol. Conserv. **115:** 131-138.

Bolten AB. 1999. Techniques for measuring sea turtles. *In* KL Eckert, KA Bjorndal, FA Abreu-Grobois, M Donnelly, eds. Research and management techniques for the conservation of sea turtles. Washington DC: IUCN/SSC Marine Turtle Specialist Group Publication no. 4, pp. 110-115.

Broderick AC, R Franenstein, F Glen, GC Hays. 2006. Are green turtles globally endangered? Global Ecol. Biogeogr. **15:** 21-26.

Broderick AC, F Glen, BJ Godley, GC Hays. 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. Oryx **36:** 1-9.

Broderick AC, F Glen, BJ Godley, GC Hays. 2003. Variation in reproductive output of marine turtles. J. Exp. Mar. Biol. Ecol. **288:** 95-109.

Broderick AC, BJ Godley, GC Hays. 2001. Trophic status drives interannual variability in nesting numbers of marine turtles. Proc. Royal Soc. Lond. B **268:** 1481-1487.

Chaloupka M, JA Musck. 1997. Chapter 9. Age, growth and population dynamics. *In* PL Lutz, JA Musck, eds. The biology of sea turtles. New York: CRC Press, pp. 233-276.

Chen S, IJ Cheng, KF Zhou, HI Wang, HX Gu, XJ Song. 2007. A comprehensive overview on the population and conservation status of sea turtles in China. Chelonian Conserv. Biol. **6:** 185-198.

Chen TH, IJ Cheng. 1995. Breeding biology of the green turtle, *Chelonia mydas*, (Reptilia: Cheloniidae) on Wan-an Island, Peng-Hu Archipelago, Taiwan. I. Nesting ecology. Mar. Biol. **124:** 9-15.

Cheng IJ. 1998. The green sea turtle in Taiwan: the reproductive biology and conservation status of an endangered species. Taipei, Taiwan: Council of Agriculture, Executive Yuan.

Cheng IJ. 2006. The ecology and the conservation of green turtles in Penghu County, Taiwan, ROC. Magung, Penghu: Penghu County Government.

Cheng IJ, TH Chen. 1994. Report on the biology of sea turtles in the nearshore waters of Taiwan (I). Taipei, Taiwan: Council of Agriculture, Executive Yuan.

Cheng IJ, PH Dutton, CI Chen, HC Chen, YH Chen, JW Shea. 2008. Comparison of the genetics and nesting ecology of two green turtle rookeries in Taiwan. J. Zool. **276:** 375-384.

Cheng IJ, ZT Lin. 1996. Ecological manual of green sea turtles on Wan-an Island, Penghu County. Magung, Penghu, Taiwan: Penghu County government.

Christens E. 1990. Nesting emergence lag in loggerhead sea turtles. J. Herpetol. **4:** 400-402.

Coleman K, LA Rothfuss, H Ota, KV Kardong. 1993. Kinematics of egg-eating by the specialized Taiwan snake *Oligodon formosanus* (Colubridae). J. Herpetol. **27:** 320-327.

Eckert KL. 1993. The biology and population status of marine turtles in the North Pacific Ocean. Honolulu, HI: National Oceanic and Atmospheric Administration-TM-NMFS-swfsc-186, SWSFC.

Foley AM, SA Peck, GR Harmann. 2006. Effect of sand characteristics and inundation on the hatching success of loggerhead sea turtle (*Caretta caretta*) clutches on low-relief mangrove island, southwest Florida. Chelonian Conserv. Biol. **5:** 32-41.

Folk RL. 1974. Petrology of sedimentary rocks. Austin, TX: Hemphill Publishing.

Glen F, AC Broderick, BJ Godley, GC Hays. 2003. Incubation environment affects phenotype of naturally incubated green turtle hatchlings. J. Mar. Biol. Assoc. UK **83:** 1183-1186.

Godfrey MH, BJ Godley. 2008. Seeing past the red: flawed IUCN global listings for sea turtle. Endanger. Species Res. **4:** (in press)

Godley BJ, AC Broderick, GC Hays. 2001. Nesting of green turtles (*Chelonia mydas*) at Ascension Island, South Atlantic. Biol. Conserv. **97:** 151-158.

Gutzke WH, GC Packard, MJ Packard, TJ Boardman. 1987. Influence of the hydric and thermal environment on eggs and hatchlings of painted turtles (*Chrysemys picta*). J. Herpetol. **43:** 393-404.

Hays GC. 2000. The implication of variable remigration intervals for the assessment of population size in marine turtles. J. Theor. Biol. **206:** 221-227.

Hays GC. 2001. The implication of adult morphology for clutch size in the flatback turtle (*Natator depressa*). J. Mar. Biol. Assoc. UK **81:** 1063-1064.

Hays GC. 2004. Good news for sea turtles. Trends Ecol. Evol. **19:** 349-351.

Hays GC, C Adams, JR Speakman. 1993. Reproductive investment by green turtles nesting on Ascension Island. Can. J. Zool. **71:** 1098-1103.

Hays GC, AC Broderick, F Glen, BJ Godley, JRD Houghton, JD Metcalfe. 2002. Water temperature and internesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. J. Therm. Biol. **27:** 429-432.

Hays GC, AC Broderick, F Glen, BJ Godley, WJ Nichols. 2001. The movements and submergence behaviour of male green turtles at Ascension Island. Mar. Biol. **139:** 395-399.

Hays GC, JR Speakman. 1991. Reproductive investment and optimum clutch size of loggerhead sea turtle (*Caretta caretta*). J. Anim. Ecol. **63:** 455-462.

Hays GC, JM Sutherland. 1991. Remigration and beach fidelity of loggerhead turtles nesting on the Island of Cephalonia, Greece. J. Herpetol. **25:** 232-233.

Hermann M, CJ Limpus, JM Whittier. 2000. The green turtle (*Chelonia mydas*): nesting trends from Heron Island, southern Queensland, Australia. *In* N Pilcher, G Ismail, eds. 2nd ASEAN Symposium and Workshop on Sea Turtle Biology and Conservation. ASEAN Academic Press Inc., London. Abstract.

Houghton JDR, AE Myers, C Lloyd, RS King, C Isaacs, GC Hays. 2007. Protracted rainfall decreases temperature within leatherback turtle (*Dermochelys coriacea*) clutches in Grenada, West Indies: ecological implications for a species displaying temperature sex determination. J. Exp. Mar. Biol. Ecol. **345:** 71-77.

Hwang WS. 1998. Preliminary studies on the forage behavior of red back pine root snake on the eggs of green sea turtle on Lanyu Island. 1998. Symposium of Animal Behaviour and Ecology, Taiwan. Nantou, Endemic Species Research Institute. (Abstract in Chinese)

Kam YC. 1994. Effect of simulated flooding on metabolism and water balance of turtle eggs and embryos. J. Herpetol. **26:** 173-178.

James MC, SA Eckert, RA Myer. 2005. Migratory and reproductive movements of male leatherback turtle (*Dermochelys coriacea*). Mar. Biol. **147:** 845-853.

Lee PLM, P Luschi, GC Hays. 2007. Detecting female precise natal philopatry in green turtles using assignment methods. Mol. Ecol. **16:** 61-74.

Limpus CJ. 1992. Estimation of tag loss in marine turtle research. J. Wildl. Res. **19:** 457-469.

Limpus CJ, JD Miller, CJ Parmenter, DJ Limpus. 2003. The green turtle, *Chelonia mydas*, population of Raine Island and the northern Great Barrier Reef: 1843-2001. Mem. Queensl. Mus. **49:** 349-440.

Limpus CJ, N Nicholls. 1988. The southern oscillation regulates the annual numbers of green turtle (*Chelonia mydas*) breeding around northern Australia. Aust. J. Wildl. Res. **15:** 157-161.

Mazaris A, Ø Fiksen, YG Matsinos. 2005. Using an individual-based model for assessment of sea turtle population viability. Pop. Ecol. **47:** 179-191.

McGinley MA. 1989. The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. Evol. Ecol. **3:** 150-156.

Miller JD. 1985. Embryology of marine turtles. *In* F Billett, P Moderson, eds. Biology of reptiles. Vol. 13. New York: J Willey, pp. 259-328.

Miller JD. 1997. Reproduction in sea turtles. *In* PL Lutz, JA Musick, eds. The biology of sea turtles. Boca Raton, FL: CRC Press, pp. 51-80.

Mortimer JA. 1995. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtle (*Chelonia mydas*). Copeia **1995:** 802-817.

Mortimer JA, A Carr. 1987. Reproduction and migration of the Ascension Island green turtle (*Chelonia mydas*). Copeia **1987:** 103-113.

Natural Conservation Society. 1988. Investigation and evaluation of the natural resources in Lanyu National Park. Taipei, Taiwan: Department of Interior, Executive Yuan.

Özdemir B, O Türkozan. 2006. Hatching success of original and hatchery nests of the green turtle, *Chelonia mydas*, in northern Cyprus. Turkey J. Zool. **30:** 377-381.

Packard GC, K Miller, MJ Packard, GF Birchard. 1999. Environmentally induced variation in body size and condition in hatchling snapping turtles (*Chelydra serpentine*). Can. J. Zool. **77:** 278-289.

Packard GC, GL Paukstis, TJ Boardman, WHN Gutzke. 1985. Daily and seasonal variations in hydric conditions and temperature inside nests of common snapping turtles (*Chelydra serpentine*). Can. J. Zool. **63:** 2422-2429.

Ratterman RJ, RA Ackermann. 1989. The water exchange and hydric microclimate of painted turtle (*Chrysemys picta*) eggs incubating in field nests. Physiol. Zool. **215:** 1059-1079.

Rivalan P, MH Godfrey, AC Prévot-Julliard, M Girondot. 2005. Maximum likelihood estimates of tag loss in leatherback turtles. J. Wildlife Manage. **69:** 540-548.

Rivalan P, R Pradel, R Choquet, M Girondot, AC Prévot-Julliard. 2006. Estimating clutch frequency in the sea turtle *Dermochelys coriacea* using stopover duration. Mar. Ecol.-Prog. Ser. **317:** 285-295.

Sato K, Y Matsuzawa, Y Tanaka, H Bando, T Minamikawa, S Sakamoto, W Naito. 1998. Internesting intervals for loggerhead turtle, *Caretta caretta*, and green turtle, *Chelonia mydas*, are affected by temperature. Can. J. Zool. **76:** 1651-1662.

Seminoff JA, K Shanker. 2008. Marine turtles and IUCN red listing: a review of the process, the pitfalls, and novel assessment approaches. J. Exp. Mar. Biol. Ecol. **356:** 52-68.

Toriba M. 1987. Feeding behaviour of two species of the genus *Oligodon* from China. Snake **19:** 5-9.

Tracy CR, GC Packard, MJ Packard. 1978. Water relations of chelonian eggs. Physiol. Zool. **57:** 378-387.

Tucker JK, NI Floramo, GL Paukstis, FJ Jazen. 1998. Response of red-eared slider, *Trachemys scripta elegans*, eggs to slightly differing water potentials. J. Herpetol. **32:** 124-128.

Yntema CL, N Mrosovsky. 1982. Critical periods and pivotal temperatures for sexual differentiation in loggerhead sea turtles. Can. J. Zool. **62:** 1012-1016.