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Observations on the Courtship and Mating Behavior of Captive Green Turtles (*Chelonia mydas*)

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Abstract.—**The courtship and mating behaviors of the Green Turtle (*Chelonia mydas*) are not well documented because of the limitations of direct observation in the ocean. We aimed to comprehensively document the courtship and mating behaviors of Green Turtles through captive observation under surveillance in the Huidong Sea Turtle National Reserve, China. In our study of 58 individuals between 2015 and 2018, we found that the turtles exhibited a polygynandrous mating system and mated during periods of rising temperatures between 20.3°–26.2° C. A single mating could last up to 16 h. The breeding temperature range for males was broader than that of females, but females had significantly longer cumulative mating time, significantly higher mating quantity, and significantly more mates than the males. The males had a similar courtship process to that of wild sea turtles. They conducted an alternating male–male competitive tactic. They focused on a few sexually receptive females and were able to accurately locate them night and day, indicating that the males may find potential mates not only by visual cues, but potentially also by olfactory stimulation.**

Key Words.—breed; competition; copulation; mate searching tactics; sea turtle

Introduction

Apart from Flatback Turtles (*Natator depressus*), sea turtles are all included in the 2018 International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2020). Detailed understanding of their behaviors is a crucial factor to be taken into consideration when drawing up effective policies for conservation management (Hooker and Baird 2001; Schofield et al. 2006). Under field conditions, the Green Turtle (*Chelonia mydas*) exhibits a courtship process of approaching, circling, climbing, and biting (Booth and Peters 1972; Okuyama et al. 2014). Their courtship behavior occurs just before the start of their nesting season and near their nesting sites (Limpus 1993). Green Turtles are likely to be generally promiscuous seasonal breeders (Limpus 1993; FitzSimmons et al. 1997). Males may spend about 30 d searching for a mate (Limpus 1993), traveling considerable distances (FitzSimmons et al. 1997). Although sea turtles have low visual acuity, males are thought to select a mate mainly using a visual cue based on size (Okuyama et al. 2014). Males also follow mounted pairs (Booth and Peters 1972) and compete for breeding females by biting mounted males as well as unmounted rivals (Limpus 1993; FitzSimmons et al. 1997; Jessop et al. 1999). A breeding female usually mates with several males (Limpus 1993; FitzSimmons et al. 1997; Chassin-Noria et al. 2017) and the copulation lasts as long as 6 h (Booth and Peters 1972).

It is challenging to study the mating behaviors of sea turtles directly in their natural habitats due to both the long-distance migration of sea turtles that limits accessibility to potential research targets (Wang et al. 2002; Xia and Gu 2012; Read et al. 2014) and environmental restrictions, such as sea depth, natural light availability, and underwater visibility, that make observing behaviors difficult. Although advanced technologies like satellite and radio telemetry, data-loggers, and animal-borne cameras, have been introduced into this field (Hochscheid et al. 2005; Myers et al. 2006; Okuyama et al. 2009, 2014), these technologies cannot describe the full range of behavioral patterns of wild animals. As a result, the courtship and mating behaviors of Green Turtles are not well documented, such as the relationship between temperature and courtship/mating events, mate-searching tactics, male-male competition strategies, male-female interactions, and the number and frequency of copulations.

Studying the courtship and mating behaviors of sea turtles under captive conditions is a feasible and intuitive method because the mating and nesting behaviors of captive Green Turtles are similar to those observed in wild populations (Wood and Wood 1980; Comuzzie and Owens 1990). Although studied in captivity, Wood and Wood (1980) mainly analyzed the correlation between

Figure 1. Research tank and closed-circuit television (CCTV) cameras used to observe the turtles mating behaviors. (Photographed by Hualing Chen).

mating duration and egg laying, and Comuzzie and Owens (1990) only analyzed the courtship components of Green Turtles. Therefore, to add to our knowledge of sea turtle mating behaviors, and to avoid research restrictions associated with studying turtles in the wild, we studied Green Turtles through captive observation under video surveillance to comprehensively understand and document the courtship and mating behaviors of this species.

Materials and Methods

Between 2015 and 2018, we studied Green Turtles mating at the Huidong Sea Turtle National Reserve (HSTNR), located in the southern area of Renping Peninsula of China (22°32′43″N, 114°53′02″W). We analyzed mating behaviors using data from 58 Green Turtles, including 43 females and 15 males with mean straight carapace length (SCL) of 85.50 ± (standard deviation) 12.06 cm (range, 64.1–112.2 cm) and 88.06 ± 6.57 cm (range, 76.6–104.4 cm), respectively. They were either wild individuals caught by local fishermen or individuals raised in HSTNR. For accurate identification, we tagged the turtles with passive integrated transponder (PIT) tags (model HPT9; Biomark, Boise, Idaho, USA), and adopted the face recognition method of Reisser et al. (2008). We measured their body lengths and weights and recorded their numbers and sex. We also took photographs of their upper, left, and right head scutes and carapace patterns under ambient and infrared light. By comparing the head scutes images and carapace patterns visually and then verifying them with the PIT chips, we found that each sea turtle had different scute and carapace features. Using these features and sex information, we could easily distinguish each mounting turtle from the video images whether it was day or night. Once identified and measured, we put all turtles in the same tank (Fig. 1), which was 60 m long, 20 m wide, and 2 m deep, at the same time in December 2014.

To reduce human disturbance and better observe the mating behaviors of the turtles, we staggered 12 waterproof Closed-Circuit Television (CCTV) cameras (model DH-SD-9A1242UA-HNI; Dahua Technology Co., Ltd., Zhejiang, China) with a starlight infrared system, 45× mechanical magnification, and a high pixel count of 1,080 evenly around the tank: half above the tank and the other half underwater. We connected the CCTV cameras to a 64-bit video recorder (model DH-NVR608-32-4KS2; Dahua Technology Co., Ltd.) with a hard disk of 16 terabyte capacity, so that we could observe the turtles mating behaviors continuously night and day. Additionally, we used HOBO Pro automatic loggers (model UA-002-64; Onset Computer Co., Ltd., Bourne, Massachusetts, USA) to record water surface temperature in a 30-min interval during 2015–2018.

To investigate the turtles mating behaviors, we replayed the image files from the CCTV cameras the following day, recording several parameters (Table 1). For each individual, we recorded the number of successful mating events (SMEs), unsuccessful mating events (UMEs), and the identity of the other turtle involved (i.e., the mate). For each UME and SME, we recorded the date and time, duration (hours), and water temperature (°C). Water temperature was also recorded every day through the year. We used UMEs and SMEs to assess breeding status (Table 1), and to quantify the length of each mating period (days) and the cumulative mating time (hours) for each individual turtle.

We used SPSS software (Version 23, International Business Machines Company, New York, New York, USA) to analyze and plot the detailed data. We performed an independent samples *t*-test to determine if there were significant differences between males and females in number of mates per mating period, number of SMEs per mating period (mating quantity), length of mating period, cumulative mating time per mating period (CMT), and water temperature at the start of mating period (first UME or SME). We also used Pearson's correlation to test the relationship between mating duration and water temperature. Average values are shown ± 1 standard deviation. Statistical significance was set at $P \leq 0.05$.

Results

***Mating frequency and mates.*—**We found that 16 of 58 Green Turtles displayed breeding status during 2015–2018: seven females (SCL = 94.04 ± 5.70 cm; range, 87.8–103.5 cm) and nine males (SCL = 91.86 ± 7.62 cm; range, 80.5–104.4 cm). Males rarely courted females < 80 cm in SCL. Males pursued females with SCL of 92.7 ± 11.1 cm (range, 81.1–112.0 cm) in a total of 175 mating events: 129 UMEs with a mean mounting duration of 0.45 ± 0.24 h (range, 0.03–1.08 h) and 46 SMEs with a mean mating duration of 7.25

Table 1. Definitions and explanations of parameters for recording and quantifying the mating behavior of Green Turtles (*Chelonia mydas*).

Parameter	Description/Explanation
Turtle Identity	Individual identified by head scale and carapace scute patterns linked to individualized PIT tag applied prior to entering tank.
Sex	Male or female identified from morphology prior to entering tank.
Size	Straight carapace length (SCL) measured prior to entering tank.
Breeding status	Male: a male that displayed mate-searching behavior and attempted to mount females (UMEs and SMEs; see below). Females: a female that was mounted by the same male more than three times in a day or courted by two or more males in the same time, totaling more than 100 min of mating. Some females we observed to be courted by a male once or twice but did not mate for the entire breeding season, and the mounting time was very short, usually within several minutes, so it was unclear whether they were in breeding status.
Water temperature	Temperature (°C) of water in tank measured every day and average over each month to estimate monthly mean water temperature (MWT) across each year of the study.
Mating Behavior	
Unsuccessful mating event (UME)	A mounting event that lasted more than 1 min, but less than 100 min.
Successful mating event (SME)	A mounting event that last more than 100 min. The interval between mating and first nesting is relatively defined, particularly for animals mating for over 100 min (Wood and Wood 1980).
Mating duration	Duration (hours) of each SME.
Mating water temperature	Temperature (°C) of water at time of each UME and SME.
Mating season	Counted if an individual has at least one SME in a given year.
Mating period	Duration (days) between first and last SME within a mating season for each individual.
Mates	Number of individuals of the opposite sex involved in SMEs each mating period for each individual.
Mating quantity	Number of SMEs per mating period for each individual (regardless of mate identity).
Cumulative mating time (CMT)	Time (hours) spent in all SMEs for each turtle in a mating period.

± 3.73 h (range, 2.13–16.0 h). Forty SMEs occurred during the day (0500–1900) and six at night (1900–0500).

One female mated in two consecutive years, while the other females mated in only one of the four years, resulting in eight female mating seasons. The largest male mated every year, while the other males mated in two consecutive years, every other year, or only once during the study period, resulting in 20 male mating seasons (Table 2). During mating seasons, females mated on average 5.75 ± 3.15 times (range, 2–11 times, n = 8), whereas males mated on average 2.30 ± 1.94 times (range, 1–8 times, n = 20; Table 2). Mating quantity (number of mating events per season) was significantly different between the sexes ($t = 5.16$, df = 7, $P < 0.001$).

Both sexes exhibited a polygynandrous mating system. We found that females mated on average with 3.25 ± 1.38 different males per mating season (range, 2–6 mates, n = 8 female seasons), whereas males mated on average with 1.30 ± 0.57 different females per mating season (range, 1–3 mates, n = 20 male seasons). Females had significantly more mates than males ($t = 6.61$, df = 7, $P < 0.001$).

Mating period and temperature.—Mating periods for females lasted 14.62 ± 5.95 d (range, 5–23 d, n = 8), resulting in an average CMT of 41.89 ± 22.13 h (range, 14.50–73.57 h, n = 8) per mating season. Conversely, mating periods for males lasted 6.5 ± 7.91 d (range, 1–23 d, n = 20), resulting in an average CMT of 16.68 ± 15.20 h (range, 2.13–60.57 h, n = 20) per mating season. Females and males were significantly different in the length of their mating period ($t = 6.10$, df = 7, $P < 0.001$) and CMT ($t = 2.87$, df = 9.99, $P = 0.017$).

The majority of mating events occurred between April and June each year, with all SMEs occurring during periods of increasing temperatures between 20.3°–26.2° C (Fig. 2A). When the water temperature was out of that range, no SMEs occurred, and the turtles, whether female or male, rarely exhibited mating behaviors. In other months with similar temperatures, but with a downward trend in temperature, we found some males attempted to court females, but no females were in breeding status, and no successful copulation was recorded.

Males started mate-searching at 19.50° ± 0.62° C (range, 18.80°–20.30° C , n = 4 males), while

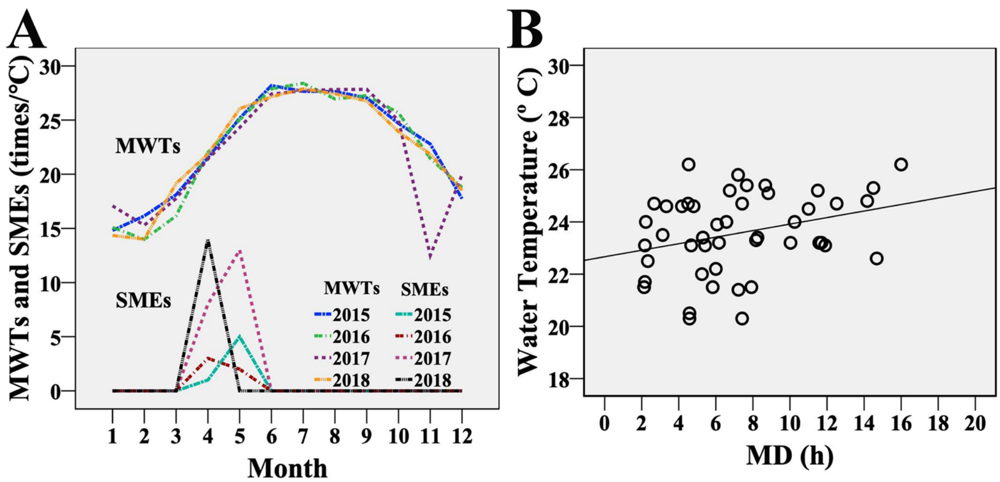

Figure 2. Water temperature effects on successful mating events (SMEs) and mating duration (MD) of Green Turtles (*Chelonia mydas*). (A) SMEs and monthly mean water temperatures (MWTs) from 2015 to 2018. SMEs occurred with increasing temperature from 20.3°–26.2° C in April and June. (B) Water temperatures during SMEs with different MD. The successful mating water temperature was 23.57° ± (standard deviation) 1.54° C (range, 20.30°–26.20° C, n = 46 SMEs) and mean individual MD was 7.25 ± 3.73 h (range, 2.13–16.00 h, n = 46 SMEs) in the past four years.

females started showing their breeding status in a water temperature of 22.27° ± 1.75° C (range, 20.50°–24.60° C, n = 4 females), which was significantly higher than males ($t = 25.62$, df = 3, $P < 0.001$). Mean water temperature for SMEs was 23.57° ± 1.54° C (range, 20.30°–26.20° C, n = 46 SMEs), but mating events concentrated between 23° and 25° C (Fig. 2A). Mating duration was positively correlated with water temperature ($r = 0.303$, $t = 30.91$, $P = 0.041$; Fig. 2B).

Male mating behavior.—All males exhibited a similar courtship process of approaching, circling, mounting, and biting a female. Breeding males blindly mounted females before any breeding female showed up; however, when there was a breeding female, they pursued it with purpose and accuracy night and day (Fig. 3A). As a result, several males generally flocked to court a breeding female at the same time, but not the other females, even if they were mature.

Table 2. Number of mates and mating quantity for each Green Turtle (*Chelonia mydas*) during each mating period/season during 2015–2018. Abbreviations are SCL = straight carapace length, F = female, M = male, and MQ = mating quantity. Blanks indicate that there was no mating event.

Turtle	SCL	2015		2016		2017		2018	
ID	(cm)	Mates	MQ	Mates	MQ	Mates	MQ	Mates	MQ
F1	94.4	4	6	2	3				
F2	90.5			2	2				
F3	103.5					4	11		
F4	93.2							6	9
F5	87.8					3	7		
F6	89.2							3	5
F7	99.5					2	3		
M1	104.4	1	2	2	2	2	4	2	4
M2	87.2	1	1	1	2				
M3	89.6	1	2			3	8	1	4
M4	91.6	1	1						
M5	87.4					1	1	1	1
M6	99.5					1	6	1	1
M7	87.4					1	1	1	1
M8	99.2					1	1	2	2
M9	80.5			1	1			1	1

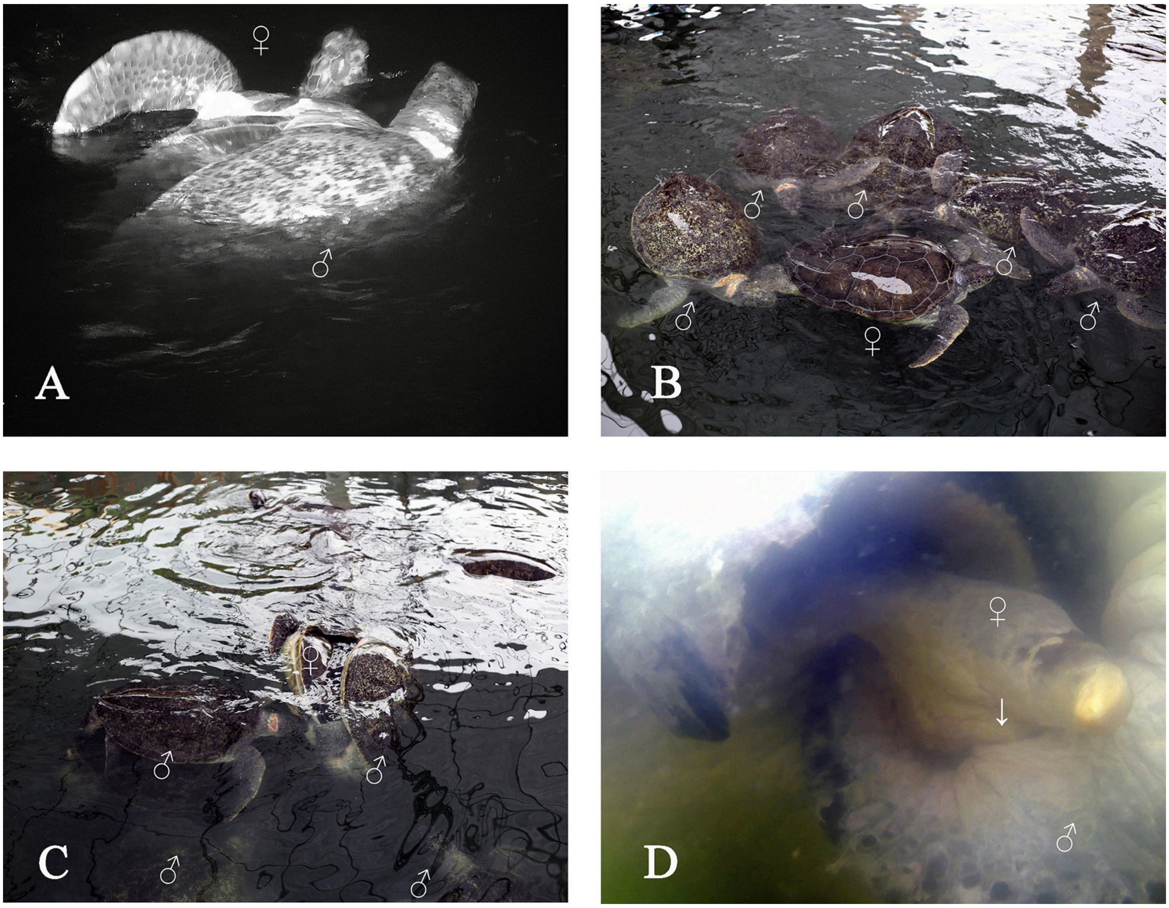

Figure 3. Green Turtle (*Chelonia mydas*) mating behaviors. (A) Male Green Turtles locating a breeding female at night. (B) Several male Green Turtles scrambling for a breeding female. (C) A crowd of males following a pair of mating Green Turtles and detaching them by biting their flippers, tail, and neck. (D) The cloacae of the couple close together as they successfully mate. Symbols are ♂: male; ♀: female; ↓: cloacae. (Photographed by Hualing Chen).

Of the 17 clearly defined courtship events during the daytime, we observed that some courting males placed their external nares and beak in the inguinal area of the courted female for a Cloacal Check and we found that there were two alternative phenomena in the competition of males. Early in the courtship, when a female attracted two or three males, the males would bite each other. A dominant male in the competition would bite the limbs, tail, and neck of his opponent to drive them away. When competing, we also observed six times a male mounted on another male, biting its neck while the male being bitten fought to escape. The losing male generally rolled their tail and swam away; however, they returned shortly afterward and, instead of fighting face to face, they followed behind the male and female pair. Afterwards, if the female attracted more than three males, we rarely found that males focused on driving their competitors away but rather on scrambling to mount a breeding female (Fig. 3B). In this case, when one of them was attempting to pair with a female, the others would detach it by biting their flippers, tail, and neck (Fig. 3C). As a result, the flippers, necks, and tails of males were scarred to varying degrees after a mating season. Once a male successfully grasped the margins of the carapace of a female with its four flippers, it did not let go readily, even when the following males were biting it severely.

Female mating behavior.—Females rejected mounting attempts by males by raising their body vertically, resisting them in a face-to-face manner, or getting behind the males and biting at their tails to drive them away. When a male mounted successfully, the female typically tightly held its hind flippers together to refuse copulation. In this circumstance, some suitors gave up temporarily, and some males attempted to conquer the breeding females by biting her neck and using his powerful tail to pry up their hind flippers. In all the daytime SMEs, we found that the hind flippers of the mounted females turned to clamp the tail of the mounting male, and the pairing turtles turned their cloacae close together to mate (Fig. 3D). After an average of 14.62 ± 5.95 d of mating (range, 5–23 d, n = 8 female mating seasons), females showed strong resistance to their mates. They were more likely to hide in some secure places and no longer accepted mates.

Discussion

All studied Green Turtles exhibited a similar courtship process comparable to that of wild populations documented by Schofield et al. (2006), Okuyama et al. (2014), and Kawazu et al. (2017). To our knowledge, we are the first to report the relationship between Green Turtle mating behavior and water temperature. We found that the mating duration of Green Turtles was positively correlated with water temperature within a certain temperature range, and Green Turtles mated during periods of rising temperatures. These patterns may be related to the levels of hormones in the turtle because the steroid hormones stimulate a carefully orchestrated period of mating receptivity (Blanvillain et al. 2010). Males exhibited reproductive activity across a wider range of temperature than the females in the present study, which could also be the difference between the effects of temperature on testosterone and estrogen in the turtles. What the relationship is between temperature and hormones of Green Turtles and whether there are regional differences related to hormone levels remains to be determined in future research.

Mate searching tactics.**—**Mate-searching is an integral part of the reproductive success of animals (Okuyama et al. 2014), but it is unknown how male Green Turtles find mates in the vast ocean. They may find potential mates by olfactory stimulation of breeding females rather than visual cues. Because Green Turtles are long-distance migratory marine animals (Wang et al. 2002; Xia and Gu 2012; Read et al. 2014), it may be challenging for males to find a mate only by vision, especially in water with poor visibility off continental coasts near nesting sites where copulation has been observed (Limpus 1993). It is also hard to explain how males could find breeding females accurately, diurnally and nocturnally, and why the males in our study focused and fought for a female but paid less attention to other females in the area. This has been observed in another study by Comuzzie and Owens (1990). It seems that male Green Turtles rely primarily on olfactory stimulation to find females, as is the case for many marine fish (Padodara and Jacob 2014). Adult female tortoises and freshwater turtles attract males also based on olfactory cues (Cagle 1950; Auffenberg 1965; Weaver 1970; Jackson and Davis 1972; Plummer 1977). Comuzzie and Owens (1990) found that male Green Turtles placed their external nares and beak in the inguinal region of recipient females, between the Rathke's gland and the cloaca, similar to male freshwater turtles, which allow them to assess the tail, cloaca, or rear portion of the shell of females (Carpenter 1966; Harless and Lambiotte 1971; Jackson and Davis 1972). Green Turtles have chemoreception sensory abilities (Bartol and Musick 2003) and males detect very minute quantities of a chemical released by females far away and locate them accurately (Manton et al. 1972). This lends strong support for our inference that Green Turtles use olfactory stimulation to find potential mates.

In some cases, breeding males have mounted divers and other larger objects that entered their territory (Bowen 2007). This may represent a strategy for breeding males to protect their territory and fight for mating privileges because we observed that some males mounted their competitors and bit their neck when they were competing for the same female. Conversely, Bowen (2007) reported that two female turtles exhibited a common response to scuba divers by moving away rapidly from the diver. This response is similar to the behavior observed in our study of the females escaping from the courtship of males. Additionally, considering that females are social during the breeding season (Schofield et al. 2006), divers are more likely to resemble male competitors than females. This supports our conclusion that during the breeding season, when breeding turtles are unable to physically distinguish the floating objects entering their mating grounds, females may generally see objects as suitors and males as potential competitors.

Visual cues are likely to be auxiliary means of mate-searching, related to the body size and other body characters of females. Our result showed that males rarely courted females < 80 cm SCL, suggesting that they can roughly distinguish mature from immature females by their body size. Despite this, body size is not the only visual cue used by males. Male Green Turtles exhibit the behavior of driving competitors away (FitzSimmons et al. 1997; Jessop et al. 1999; Schofield et al. 2006), which also supports the ability of males to distinguish between males and females. This recognition of different sexes would be impossible to achieve by body size alone. Moreover, Auffenberg (1965) observed that Yellow-footed Tortoises (*Geochelone denticulata*) and Red-footed Tortoises (*G. carbonaria*) could distinguish both adult males of the same species and any other turtles through head movements. This also suggests that Green Turtles may have some other visual cues, such as body characters and behavior.

Based on the existing information, we think that the male Green Turtles may first use olfactory stimulation to guide direction to mates. When there are turtles in front of the scent guide and where the concentration of olfactory stimulation is not enough for them to locate the breeding females, the males may use visual cues, such as size, shape, and other body characteristics, to determine whether the turtles are of the same species, female or male, and mature or immature. Then, they may make tentative advances to a female that exhibits characteristics similar to those of a breeding turtle before actually finding a breeding turtle. This leads to the phenomenon of males blindly pursuing females, as mentioned in studies by Okuyama et al. (2014) and Schofield et al. (2006); however, when males can locate a breeding female by olfactory stimulation, they may pursue it aggressively with purpose. Nonetheless, these inferences also need to be confirmed by further research.

***Mating strategies.*—**During courtship, males exhibited different mating behaviors when the number of competitors increased. This may represent alternative mating strategies for males to increase their reproductive chances because individuals may have a conditional mating strategy based on external factors, such as available mates and nearby competitors (Shuster 2002; Gross 1996), that allows them to maximize their fitness (Gross 1996) and increase reproductive success (Dominey 1984). When there are only one or two competitive turtles, there may be a high chance of a stronger male among them adopting a mate-guarding strategy to get the mating advantage. In contrast, when there are a high number of many competitors, the mate-guarding strategy may no longer be effective, and even a strong male could not guarantee the mating advantage. Therefore, males were no longer focused on expelling competitors but on scrambling for the breeding female over which they fought. We found that the SMEs comprised approximately one-third of the UMEs, suggesting that the mating advantage was dependent upon the male grabbing the carapace of the breeding female with four limbs, which agrees with results found by Kawazu et al. (2017). Varying levels of reproductive success will select for phenotypes and strategies to maximize the chance of an animal obtaining a mate (Shuster 2002). Long mounting times, such as over 16 h in the present study and 119 h in Wood and Wood (1980), may also represent a male strategy for protecting their mating advantage, but it needs to be further explored.

The polygynandrous mating system is also a strategy for Green Turtles to adapt to the environment and produce more offspring. To make up for the long maturity period of about 20–40 y (Goshe et al. 2010; Avens et al. 2015), slow reproductive cycle of 2–6 y (Troëng and Chaloupka 2007), and high mortality of hatchlings (Fosdick and Fosdick 1994), sea turtles need to produce as many offspring as possible to ensure a sustainable population. Energy acquisition and allocation, however, play critical roles in determining reproductive output (Wyneken et al. 2013). We found that males have lower mating quantity, smaller CMT, and fewer mates than females, suggesting that male Green Turtles may generally store less reproductive energy than females. This may be due to the considerable energy expended during the long-term mate-searching period in which a male generally spends about 30 d (Limpus 1993) traveling considerable distances for a mate (FitzSimmons et al. 1997), and fierce mating competition. Accordingly, in general, the fertility of a male may not meet the maximum reproductive need of a female. In this case, the polygynandrous mating system may ensure maximum reproductive output for both sexes.

***Mating success depends on the females.*—**According to the results, the mating success of sea turtles may be determined by females. First, the females were mated only during mating seasons, and no SMEs were recorded outside the seasons. Second, the SMEs comprised approximately one-third of the UMEs, indicating that, even if the females were in breeding status, they did not always accept all the pursuits of males. Third, the females that were not in breeding status did not accept mating throughout the year. Finally, previous researchers only reported the copulation occurring just before the breeding season, but rarely in other seasons (Wood and Wood 1980; Limpus 1993; Kawazu et al. 2017). All these phenomena support our interpretation. Our study provides valuable biological evidence for a better understanding of the courtship behavior and for the development of conservation strategies that involve artificial breeding management of Green Turtles. Additionally, this study also suggests potential avenues for future research, such as examining how turtles find sexual partners and the relationship between mating behavior and sex hormone regulation.

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