difference was identified in beach width between beaches in the northern and southern regions of Okinawajima (t-test: $P > 0.05$).

Discussion. — The number of body pits per km shore-line in the northern half of Okinawajima (4.65) was ca. 19 times greater than that in the southern half of the island (0.24). This variable merely reflects the total number of nesting attempts per km shore-line, and thus might not strictly correlate with the actual nesting frequency. However, such a prominent difference should be interpreted as indicative of much greater importance of beaches located in the northern part of the island than those in the southern part as nesting sites. The number of body pits per km in the other islands (3.20) was lower than that in northern Okinawajima, but much higher than that in the southern half of Okinawajima. The number of body pits found on adjacent islands (57) equaled 39% of the total found in the present survey. Thus, these islands also seem to offer important nesting sites for sea turtle populations around the Okinawa Islands.

Hays and Speakman (1993) found that in Greece the loggerhead turtle tends to lay eggs away from the sea, and that the hatching success increases significantly in nests laid farther from the sea. This means that the width of beaches can be an important factor for sea turtles emerging on beaches to nest. Therefore it is suggested that sea turtles prefer wider beaches, resulting in the presence of a significant correlation between the pit density and the beach width in our data.

As was mentioned above, however, there was no significant difference in width between beaches of the northern and the southern regions of Okinawajima. So, one cannot attribute the striking difference in the density of nesting traces between these regions to beach width. On Ascension Island, nesting frequency is reported to be less on beaches near civilization (Stancyk and Ross, 1978). Many types of artificial lighting also have the potential to disrupt the nesting of sea turtles (Witherington, 1992). The southern regions of Okinawajima accommodate a much greater human population and have more facilities for tourists than the northern portion (National Geographic Agent of Japan, 1990). Thus, disturbances to nesting sea turtles in the southern regions are probably much greater than in the northern portion. Collection and analyses of data for artificial obstructions, as well as for natural beach characteristics other than those considered above (Mortimer, 1982), are strongly needed to verify this hypothesis and to advance conservation measures for nesting sea turtles in the central Ryukyus.

In this survey, the confirmation of the presence of eggs or species identification was not made for each body pit because of time limitations. In the future, efforts to search for eggs will be necessary to solve these problems.

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Mating Behavior in Captive Alligator Snapping Turtles (*Macroclemys temminckii*)

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There is no information about mating or courtship behavior of alligator snapping turtles (*Macroclemys temminckii*) in their natural environment and only limited information exists about captives (Allen and Neill, 1950; Dobie, 1971; Grimpe, 1987). Described mating behavior occurs in the water where the larger male pursues the smaller female. After a short pursuit the male climbs onto the female's carapace and grasps the front and back margins. The chin of the male touches the back of the head of the female, and the female may bite the male around the head region. Duration of coitus is from 5 to 25 minutes. The male's body is slanted to one side with the tail pushed downward which pushes the female's tail aside, allowing

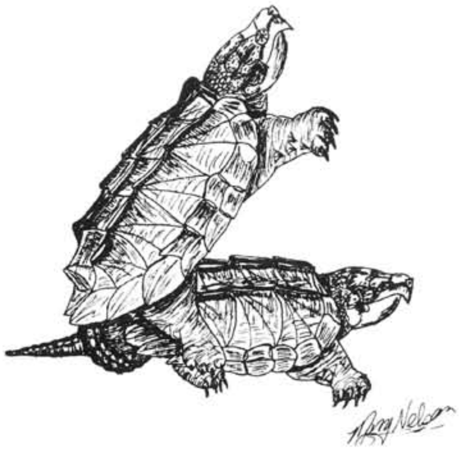

Figure 1. Vertical posture by male during coitus.

contact. Similar mounting occasionally occurs during feeding periods.

At the conclusion of a feeding study in the spring of 1992, we observed mating behavior in captive *M. temminckii*. Behavior we observed was similar to that reported by Allen and Neill (1950) and Grimpe (1987), but some behavior has not been previously reported. Our objectives in this study were to add new information to the natural history of *M. temminckii*, as well as describing its mating behavior in relation to other turtle species.

Materials and Methods. — Turtles used in this study inhabited two round, ground-level polyurethane tanks, 1 m deep, 2.9 m in diameter (7600 liters) at Northeast Louisiana University's Turtle Research Area in Monroe, Louisiana. Water from outside faucets freely circulated in the tanks. Tarpaulins provided shade during summer. Wooden planks provided cover and ramps for turtles to exit tanks. Dimensions of the overall enclosed facility were 18.3 x 27.4 m.

During a winter feeding study turtles were placed into all male or combined female and subadult groups. On 10 March 1992, after six months of separation from each other, 7 adult males and females were placed into heterosexual groups in two different tanks in male:female ratios of 2:1 and 2:2. Tank 1 contained two males weighing 38.6 and 44.5 kg with a newly captured 19.5 kg female. Tank 2 contained two males weighing 31.8 and 33.1 kg and two females weighing 11.8 and 16.3 kg. Observations were documented with video allowing us to observe mating activity in detail. Most observations were taken from a vantage point overlooking the turtles. Ten observations were made by day and night, averaging 4.3 hrs per observation (range 1–10 hrs) for seven consecutive days, after which mating activity appeared to cease. Nocturnal observations were made with a Noctron V model 9878A infrared night scope.

Results. — The first observed mating occurred in Tank 1 between 0035 and 0300 hrs on 10 March 1991 (Table 1), involving the 44.5 kg male and the 19.5 kg female. Mating occurred near the bottom of the tank. The male was positioned on top of the female with his plastron resting on top of her carapace. The forefeet of the male were positioned anteriorly at the level of the bridge of the female's shell while his hind feet grasped the rear margins of her carapace. In this position the male was able to control the movement of the female. The male's tail was wrapped underneath the female, whereas the female's tail was horizontal and positioned slightly toward her right side. The male's head was pointed downward and he frequently pushed his nose into the back of the female's neck and also positioned his head in such a manner that his chin rested on top of her head. Both turtles rocked from side to side with the male making quick bites to the back of the female's neck. The male made upward thrusting motions with the tail until intromission occurred. Several bites were exchanged at this time. Bites by the female appeared to be more aggressive than bites by the male. The female then moved slightly, and the male released the grip of his forefeet. However, he continued to hold her in position with his hind feet and then floated vertically in the water and maintained a rigid posture for several seconds (Fig. 1). The turtles then parted, with their tails separating last. Coitus lasted approximately six minutes. Following copulation the male made numerous attempts to remount the female but was unsuccessful, often waiting at her side. He also pursued the smaller 38.6 kg male in an aggressive manner and mounted him in the same fashion as he had mounted the female, even wrapping his tail underneath the other male. He bit the smaller male severely and in turn the smaller male aggressively bit the larger male. The pursuit of

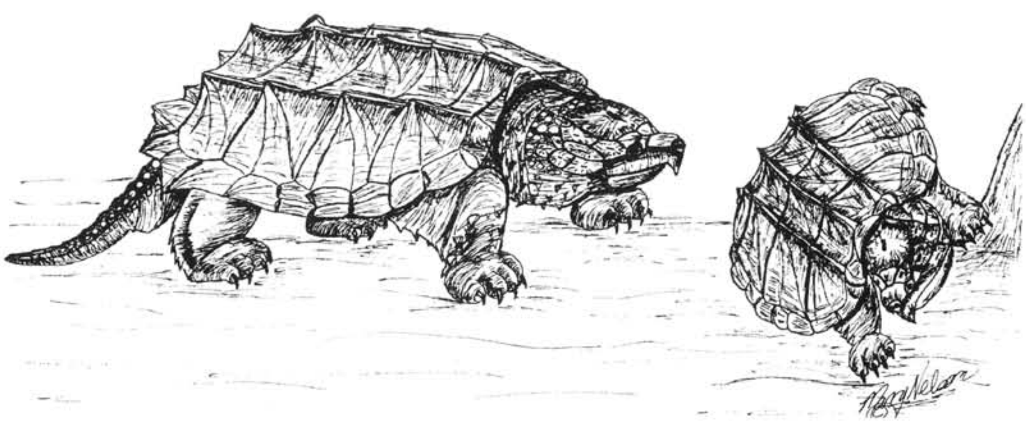

Figure 2. Carapace orientation (lateral tilting) by female.

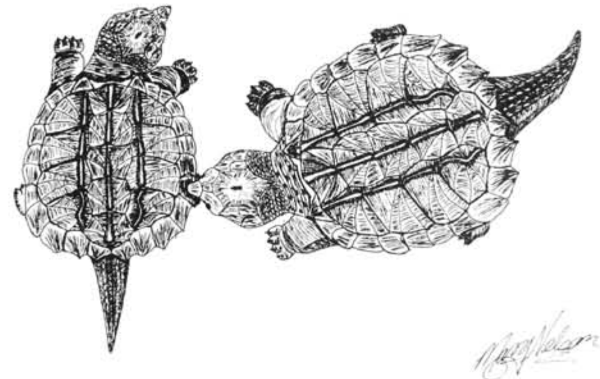

Figure 3. Olfactory sniffing of carapace bridge by male.

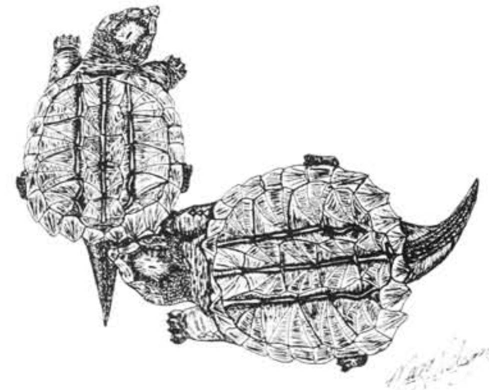

Figure 4. Olfactory sniffing of cloaca region by male.

the smaller male by the larger male did not cease until the smaller male rose to the surface of the tank and floated.

Failed attempts at mating were also observed (Table 1). This usually occurred when a small female successfully eluded a much larger male. Mating activity decreased approximately 72 hours after the heterosexual grouping was established. Water temperature during the most intense periods of mating activity was 16.0ºC, but breeding activity seemed to decline as the water temperature reached 18.0ºC. Mating activity was most intense in the evening and throughout the night.

Mating attempts by a 31.8 kg male with a 16.3 kg female occurred in Tank 2 and followed a similar pattern (Table 1). In almost all observed or attempted matings the following behavioral sequence occurred: antagonistic behavior or actual combat between males; apparent olfactory exploration (sniffing) of a female by a male; waiting, mounting, or attempted mounting; copulation (unless the episode was terminated by the female); and pursuit of the female by the male.

Females occasionally exhibited behavior that appeared to be possible courting of the dominant male by approaching him from the rear. Avoidance behavior of the dominant male was demonstrated by carapace tilting, fleeing, remaining at the surface of water, and biting. Submissive males would make an occasional approach toward a female and avoid the dominant male.

When two males were placed in a tank with one or two females, only one male attempted mating. However, if two different dominant males were placed together with a receptive female, both males would attempt mating and combat usually occurred (Table 2). The dominant male always pursued and, if possible, mounted the submissive male before attempting to mate with a female. Dominant males held subordinate males on the bottom, and the subordinate males struggled to surface for air. Both males bit each other in an aggressive manner. Combat ended only when the less aggressive male escaped from the dominant male. Size did not appear to be a major factor in the establishment of dominance or to provide a major advantage in mating success.

Males were observed making large nasal expulsions of air (bubbling) (Tables 1 and 2). This did not seem to be just a release of air, but instead a forceful expulsion. As air was forced from the nostrils, the water surface above the turtle bubbled dramatically. Air expulsion was only observed among males when one male was approaching another in an aggressive posture, or when a male was apparently smelling a female.

Both females and males utilized carapace orientation (lateral tilting). Frequently when a female was approached by a breeding male, she turned on her side, oriented her carapace toward the male and became lateral in the water (Fig. 2). Submissive males also behaved in this manner. In

Table 1. Mating observations of captive male and female *Macroclemys temminckii*.

Obs. No.	Date	Time	Water Temp.	Weight kg ♂/♀	Sniffing	♂ Pursuit	♀ Avoidance	♀ Lateral Tilting	Bubbling	♀ Initiation	Mounting	Coitus
1	3-10-92	0035-0300	16.0C	44.5/19.5	++	++	++	+			++	+
2	3-10-92	1000-1815	16.0C	44.5/19.5	+++	++	+	+	+		+++	+
				31.8/16.3	+		+				+	
3	3-11-92	2200-0000	16.0C	44.5/19.5	+++	+	+	+		+	+	
4	3-12-92	1000-2000	16.0C	44.5/19.5	+++	+	+	+	+	+	++	
		2200-0100		31.8/19.5	++			+			+	
				44.5/19.5	+	+	+	+			+	
5	3-13-92	1100-1830	17.0C	44.5/19.5	+		+	+				
6	3-14-92	1100-1400	18.0C	44.5/19.5	+		+	+				
		2300-0000		44.5/19.5	+		+					
7	3-15-92	1515-2000	18.5C	44.5/19.5	+		+	+			+	
				31.8/19.5			+					
8	3-16-92	2230-2310	17.0C	44.0/19.5	++		+	+				
				44.5/16.3	+	+	+				+	

Table 2. Observations of aggressive interaction between male *M. temminckii.*

Observ.	Date	Time	Water Temp.	Weight (kg) Dom/Sub	Bubbling	Lateral Tilting	Biting	Combat	Pursuit/ Fleeing
1	3-10-92	0035-0300	16.0C	44.5/38.6		++	+		++
2	3-10-92	1000-1815	16.0C	44.5/38.6	+	+	+	+	+
				31.8/33.1		+	+	+	+
3	3-11-92	2200-0000	16.0C	44.5/38.6	+	+			
				31.8/33.1		+			
4	3-12-92	1000-2000	16.0C	44.5/36.8		+	+		+
				31.8/44.5	++	+	+		
				44.5/31.8		+	+	+	+
				31.8/38.6		+			++
5	3-12-92	2200-0100	16.0C	44.5/31.8	+	++	+	+	+
6	3-13-92	1100-1830	17.0C	44.5/31.8	+	+	+	+	+
7	3-14-92	1100-1400	18.0C	44.5/31.8			+		+
		2300-0000		44.5/31.8		+			
8	3-15-92	1515-2000	18.5C	44.5/31.8		+			+
9	3-16-92	2230-2310	17.0C	44.5/31.8		+			+

addition, the behavior was observed during feeding, but not as frequently as during peak mating activity (Tables 1 and 2).

During the first three days of mating activity, apparent olfactory investigation (sniffing) was observed in both males and females, however, males were observed investigating females more frequently (Table 1). Males usually began what appeared to be smelling at the nose of the female. They then moved toward the rear of the female, apparently smelling down the length of her carapace and along the bridge, eventually stopping near the cloaca. Often they made lengthy investigations along the dorsal side of the base of the female's tail and at the eighth, ninth, and tenth marginals (Figs. 3 and 4). One female (19.5 kg) seemed to initiate courting activity by approaching a 44.5 kg male (Table 1). She appeared to explore his cloaca and then climb onto his back, but not in a mating posture. During one such episode, the male began to walk around the tank while the female remained on his back. When the male turned to face the female she moved away.

Discussion. — Breeding behavior in *M. temminckii* is similar to published accounts of other bottom-walking turtles: *Chelydra*, *Kinosternon*, and *Sternotherus* (Lagler, 1941; Legler, 1955; Mahmoud, 1967; Gans and Tinkle, 1977; Murphy and Lamoreaux, 1978; Cox et al., 1979; Seigel, 1980; Baker and Gillingham, 1983; Bels and Crama, 1994) except for those species in which the males are smaller than the females. Berry and Shine (1980) stated that in bottom-walking turtles courtship does not occur and insemination is forced upon the female. Pritchard (1989) also stated that courtship probably does not occur among *M. temminckii* and that copulation was forced upon the smaller female by the larger male. Bels and Crama (1994) classified three motor patterns that often occur in turtle mating behavior: premounting courtship (approach/chase, sniffing, intersexual motor patterns, mount, and copulation), intermediate courtship, and a mounting courtship display (approach/chase, sniffing, mount/intersexual motor patterns, and copulation). Using this classification we place *M. temminckii* in the group showing mounting courtship display.

The mating of *M. temminckii* shows parallels with that of *Sternotherus* and *Kinosternon* in several aspects such as bridge and cloacal sniffing, mounting, trailing, fleeing, and biting (Mahmoud, 1967; Pritchard 1979, 1989; Bels and Crama, 1994). Sniffing was directed towards the eighth and tenth marginals on *M. temminckii* and seventh and eighth marginals on *S. minor*.

In Tank 1, the female never approached the submissive male, but did approach the dominant male, and it appeared that she had made a mate selection in doing this. Females easily escaped from males on many occasions, and this suggests that female participation may, to some extent, be facilitated by male courtship.

Air expulsion (bubbling) may be a manifestation of excitement, or a threat display by the males, or even a method employed to reduce buoyancy. Decreased buoyancy may enable males to control a female on the bottom while copulating or to hold another male below the surface while in combat. Taylor (1933) reported that when *Chelydra serpentina* face each other during courtship, air is gulped and then forced through the nostrils, causing the water to "boil" above their heads and Gans and Tinkle (1977) considered this a courtship behavior in *C. serpentina*.

Prior to the present study, bubbling, female courtship, lateral tilting, olfactory sniffing, and the rigid, vertical posture exhibited by males during coitus had not been reported in *M. temminckii*.

Lateral tilting of the body maximizes protection afforded by the carapace, and by tilting, a turtle is more likely to keep another turtle off its carapace. A similar "refusal" posture has also been noted in green sea turtles (*Chelonia mydas*) (Booth and Peters, 1972). However, with *C. mydas* the refusal position is vertical rather than lateral.

Olfactory "sniffing" may serve a necessary function in mating activity of *M. temminckii*, such as distinguishing males from females, but the behavior could also be used by the turtles to distinguish one individual from another. In areas where turtles are few, pheromones may serve an important function in males locating females. Our data did not allow us to test if these turtles were actually undertaking an olfactory evaluation, or whether pheromones play a role in the behavior.

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Meat on the Move: Diet of a Predatory Turtle, *Deirochelys reticularia* (Testudines: Emydidae)

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The chicken turtle, *Deirochelys reticularia*, is a characteristic but rarely abundant inhabitant of shallow, lentic waters in coastal lowlands of southeastern United States. Inadequate knowledge of its diet has led to widespread speculation that the species is broadly omnivorous (Carr, 1952; Campbell, 1969; Ernst et al., 1994), although a few authors (Jackson, 1978, 1988; Pritchard, 1979) have suggested a more strictly carnivorous diet. Very limited evidence supporting the latter position is provided by Marchand (1942), Carr (1952), and Mitchell (1994), who reported glass shrimp, crayfish, tadpoles, a snail, a beetle, and only a trace of aquatic plants in chicken turtle natural diets.

Methods. — In conjunction with a study of the reproductive biology of the species (Jackson, 1988), I examined the gut contents of 24 chicken turtles; feces were collected from another that was retained alive for behavioral study. The sample included five adult males (103–137 mm plastron length [PL], 192–448 g), 19 adult females (147–190 mm PL, 645–1410 g), and one subadult female (137 mm PL, 410 g) collected from 1974 to 1977; shells of 12 were deposited in the Florida Museum of Natural History herpetology collection (UF 37555, 44210–44216, 44218–44220, 44231). All but one of the turtles were collected on land, either in association with nesting activity or with terrestrial wandering that presumably represented migration between bodies of water; several specimens were road-kills. Most of the turtles were from Alachua County (12) or nearby counties (Baker, Dixie, Levy, Putnam, and Marion) in northern peninsular Florida, where the subspecies *D. r. chrysea* and *D. r. reticularia* intergrade. The sample also included one specimen from the Florida panhandle (Wakulla County), two from the Florida east coast (Brevard County), and two from southern Georgia (Ware and Charlton counties). The entire alimentary tract of each animal was examined fresh