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A QUANTITATIVE ANALYSIS OF COURTSHIP BEHAVIOR IN CAPTIVE GREEN SEA TURTLES (*CHELONIA MYDAS*)

DIANA K. CROWELL COMUZZIE[1,2] AND DAVID WM. OWENS[2]

[1]*Department of Biology, Texas A&M University, College Station, TX 77840, USA*

ABSTRACT: Reproductive behavior of captive green sea turtles (*Chelonia mydas*) was observed at the Cayman Turtle Farm, British West Indies. Observed components of courtship behavior included gular rubbing, biting, cloacal checking, circling and biting, chasing, following, attempted mounting, mounting, and escorting. Data analysis indicated that in each of the observed components, reproductively attractive females were the target of the behavior significantly more often than reproductively nonattractive females. Cloacal checks may be used by both males and females to assess reproductive condition of females. Males may escort mounted pairs to disrupt copulation attempts by rivals and increase their own reproductive success; females may act as escorts to enhance later mate availability. In general, females appear to signal approaching reproductive receptivity to males, but females may exercise mate selectivity by avoiding mounting.

Key words: Sea turtle; *Chelonia mydas*; Courtship behavior

MATING and courtship behaviors of marine turtles are not well documented. Indeed, except for nesting and hatching, what is known about marine turtle behavior comes almost entirely from reports of incidental observations. However, in two publications (Booth and Peters, 1972; Bustard, 1973) marine turtle courtship has been described in general but not in detail.

Bustard (1973) reported a courtship sequence for *Chelonia mydas* consisting of the male facing and nuzzling the female, then biting her neck and rear flippers, and finally chasing her if she swam away. If a female was in water deeper than the height of her carapace, a male was able to mount by swimming onto her back and hooking his foreflipper claws over the anterior rim of her carapace. A female could avoid mounting by entering shallow pools where males were unable to mount her highly domed carapace. Booth and Peters (1972) reported similar behavior in *Chelonia mydas*, and added observations of circling and biting by females as well as a female "refusal" position. In the "refusal" position, an unreceptive female presented her plastron vertically to an approaching male. Although both reports provided valuable data

[2] PRESENT ADDRESS: Department of Systematics and Ecology, 3038 Haworth Hall, University of Kansas, Lawrence, KS 66045-2106, USA.

on wild cheloniid behavior, they lacked objective quantification. It is unclear how often individual components occurred, and if they were related to courtship or daily, nonreproductive, activity.

The objective of this study was to evaluate systematically and quantitatively selected components of marine turtle reproductive behavior. Observations were statistically analyzed to determine if the components were specific to reproduction, and then critically evaluated in light of reports of specific behaviors in the turtle literature.

Methods

Subjects

Chelonia mydas were maintained yearround at Cayman Turtle Farm, Ltd., Grand Cayman Island, in a 26 m × 61 m (2.25 million liters), outdoor, rectangular breeding pool containing natural sea water. Three sides of the pool were formed from the existing calcareous substrate, and the fourth side of the pool by a 720 m^2 artificial nesting beach which sloped down to form the floor of the pool. Maximum depth of the pool was 2.8 m (Wood and Wood, 1988).

We observed 181 *C. mydas* in two interconnected sections of the large pool. All animals in the study were marked with large, numbered tags which allowed accurate identification of individuals. Managers of the turtle farm maintained strongly female-biased sex ratios in the sections in an attempt to increase breeding potential: section A contained 12 males and 66 females while section B contained 16 males and 87 females. These numbers may or may not reflect natural conditions, because very little is known about the densities and sex ratios of wild populations. However, skewed ratios and very high densities of nesting *Chelonia mydas* and immature *Caretta caretta* have been noted (Limpus and Reed, 1985; Wibbles et al., 1987). The captive turtles were predominantly in the weight range of 100–150 kg, with a few females up to 230 kg. Turtles in sections A and B were captured in the wild as adults between 1969 and 1977 (Wood and Wood, 1980). All *C. mydas* at the farm were fed a high protein commercial pellet twice daily, in the morning (about 0800 h) and in the afternoon (about 1600 h).

The mating season in *C. mydas* extended from March until July, but peaked in May and early June (Licht et al., 1985). The nesting season began while mating was still occurring and lasted until September or October (Ulrich and Parkes, 1978). The personnel at the Cayman Turtle Farm continuously monitored the breeding animals from March–August to record all participants in mating and nesting, but not detailed notes on specific behaviors.

Observations

The observations reported here were made over three breeding seasons. *Chelonia mydas* was observed 17–30 May and 19–25 June 1984, 3–18 May 1985, and 12 May–2 June 1986. In 1984, observations were made periodically throughout the day. In 1985 and 1986, observations were made twice per day, from just before dawn (0600 h) until about 1000 h, and from about 1430 h until dark (about 1830 h). These observation periods reflected the turtles' activity periods (as well as those of wild turtles) (Mendonca, 1983), because the turtles were largely inactive during midday. Over the three seasons, turtles were watched more than 450 h on 58 days. Data from the 1984 season were used to identify the specific components of reproductive behavior, which then formed the categories for the analysis of the 1985 and 1986 data. Only data from 1985 and 1986 are reported here. All types of behaviors (e.g., courtship, social, grooming) were recorded by the continuous recording method (Martin and Bateson, 1986).

Data Analyses

If some types of male behavior are specific to courtship, they should be directed significantly more often towards females during periods when definitive reproductive behaviors such as mounting and copulation occur than at other times. We found that Wood and Wood's (1980) description of a "heat" period included only female receptivity, and was too narrow to include the early male courtship behaviors that we

observed. Data from 1984 indicated that females were initially attractive, but not receptive, to males although they did nothing to solicit male attentions. In fact, females initially ignored or repelled male courtship by biting, swimming away, or beaching themselves.

Females did not initiate interactions as often as males did. Over the entire 1985 and 1986 seasons, males initiated 943 interactions with females, but females initiated only 251 interactions with males. Therefore, to define an activity period that accurately encompassed both female attractiveness and receptivity, the 1985 mating activity of 40 females was plotted (Fig. 1). For each female, the total number of minutes she was mounted by males on each day (a measure of her attractiveness) was plotted, with the female's day of maximum mating corresponding to day zero. Most mounts occurred between five days pre-maximum mating and 10 days post-maximum mating (Fig. 1). Therefore, for the purposes of this research, the term "breeding" was used to define that 16-day period. Although most females nest several times, they usually only mate during one period, and thus, only had one breeding period per season (Owens, 1980). "Nonbreeding" was used to describe the female's condition during the remaining portions of the mating season. Additionally, females that did not mate during a nesting season were described as nonbreeding. Female *C. mydas* do not commonly mate ever year (Limpus and Fleay, 1983), so it is not surprising that there should be a number of nonbreeding females in any given year.

In the statistical analyses, we compared behaviors of breeding females to behaviors of nonbreeding females for each behavioral component. Since entire breeding and nonbreeding intervals were not observed for all females, raw counts of specific components of courtship behavior were standardized by dividing the number of times a female performed the component by the total number of observed days she was in a breeding interval (or nonbreeding). Females were ranked by the frequency with which each courtship component was performed. Ranks of females in breeding and nonbreeding intervals were compared by Mann-Whitney *U*-tests.

Spearman's coefficient of rank correlation was used to evaluate the relationship between copulation interference and reproductive success in males. Each male was ranked according to the frequency with which he interfered with copulating pairs, and this rank was matched to his rank in frequency of mounts. The relationship between copulation interference and reproductive success in females was evaluated using Student's *t*-test. The mean number of minutes interfering females were mounted was compared to the mean number of minutes females that did not interfere were mounted. These data were subjected to a log transformation due to high variances relative to the mean. A Chi-square Goodness of Fit test was used to determine if females interfered before or after their breeding period. The number of females that interfered before their breeding period was compared to the number of females that interfered after their breeding period. All statistical tests were taken from Sokal and Rohlf (1981).

Results and Discussion

The following components are selected steps in the courtship sequence and are listed in the approximate order in which they occurred.

Gular rub.—Gular rubs occurred when a male or female rubbed its gular region along a recipient's head or carapace. Males gular rubbed breeding females significantly more than they rubbed nonbreeding females. Nonbreeding females also gular rubbed breeding females significantly more than they rubbed other nonbreeding females (Table 1). There was only one record of a gular rub by a female on a male, and only one record of a gular rub by a breeding female on a nonbreeding female.

Bite.—One of the most common courtship components was biting, and its milder form, nipping. In nipping, smaller amounts of the recipient's skin were taken into the mouth. Turtles were bitten all over the body, but especially in the soft skin areas around the shoulders, neck, and around

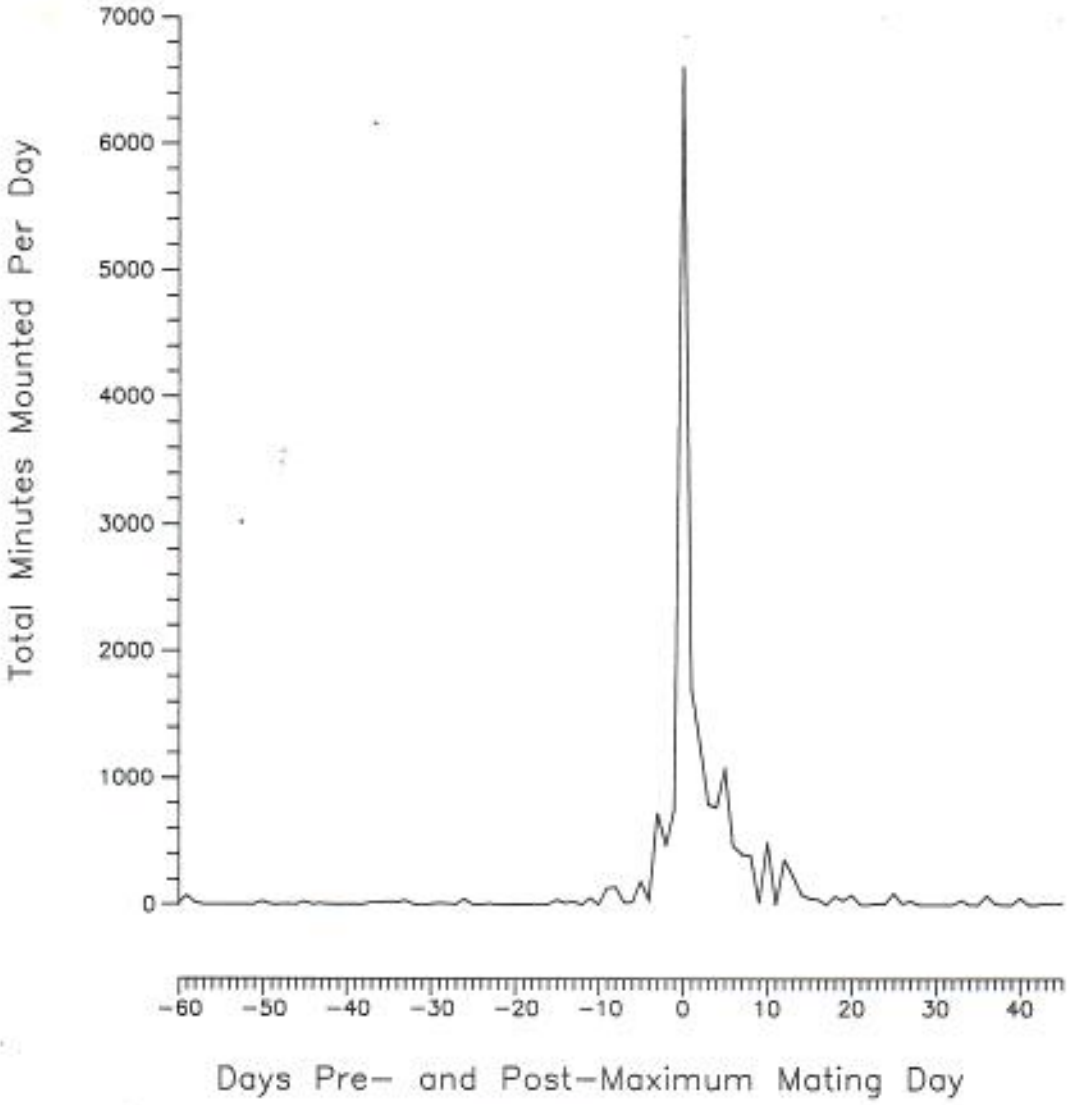

FIG. 1.—Time mounted by males relative to days of maximum mating for 40 females.

the mouth. Fresh bite scars were not seen after the mating season. Biting by males and females was described by Booth and Peters (1972) as a non-aggressive prelude to mating, and similarly was suggested by Bustard (1973) to be an extension of nuzzling which induces female arousal. Male *C. mydas* bit breeding females significantly more than they bit nonbreeding females, and breeding females bit males significantly more than nonbreeding females bit males (Table 1).

Cloacal check.—A cloacal check occurred when the external nares and beak of a turtle were placed in the recipient turtle's inguinal region, between the Rathke's gland and the cloaca. In freshwater species of turtles, the tail, cloaca, or rear portion of the shell may be sampled by males (Carpenter, 1966; Carpenter and Ferguson, 1977; Harless and Lambiotte, 1971; Jackson and Davis, 1972*a*,*b*); however, this behavior has not been previously reported in marine turtles. Bustard (1973)

TABLE 1.—Descriptive statistics for observed components of courtship behavior. n = number of individuals displaying the behavior, $\bar{x}$ = mean standardized number of occurrences of the behavior (data standardized by dividing raw counts by the number of days in the breeding or nonbreeding state), SE = one standard error of the group mean. z scores calculated from Mann-Whitney U-test.

	Breeding females			Nonbreeding females				
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	z	P
Male gular rubs	5	0.172	0.045	7	0.075	0.002	2.84	0.005*
Female gular rubs	2	0.276	0.109	10	0.085	0.008	2.15	0.032*
Male bites	24	0.500	0.153	63	0.143	0.155	4.68	0.00002*
Female bites	19	0.292	0.088	42	0.137	0.013	3.66	0.0003*
Male cloacal checks	9	0.344	0.133	11	0.105	0.013	2.47	0.014*
Female cloacal checks	7	0.198	0.039	9	0.073	0.002	3.33	0.001*
Male circle and bites	20	0.376	0.12	28	0.136	0.022	2.55	0.011*
Male chases	14	0.446	0.520	24	0.128	0.120	4.92	0.00001*
Male attempted mounts	30	0.712	0.243	67	0.132	0.020	5.23	0.00001*

* Significant difference at $\alpha = 0.05$.

described loose biting of the rear flippers by males which may be somewhat similar to cloacal checking. In our study, both males and females checked the cloacas of breeding females significantly more than they did nonbreeding females (Table 1).

Circle and bite.—Male turtles continually swam around to the backs of females in order to mount. A female, however, would counter the male's movements so that she continually faced him, and thus avoided being mounted. This resulted in the female turning in a circle. During this circling, females bit males, which caused males to withdraw. Also during circling, males often bit the female's neck, which held her in place while he mounted from the side. Similar circling behavior was reported by Booth and Peters (1972). Males circled and bit breeding females significantly more than they did nonbreeding females (Table 1). Bites that occurred during circle and biting were not also included in the counts of bites.

Chase.—A female may break out of the circling and biting mode and swim rapidly away (>1 m/s), as may a female being disturbed in some other way. This movement appeared to incite most of the males and other females in the section to chase her. Both Booth and Peters (1972) and Bustard (1973) reported females fleeing at speed and being pursued by males. At the turtle farm, slower following (<0.20 m/s) also occurred, but usually involved only two animals. Males chased breeding females significantly more than nonbreeding females (Table 1).

Attempted mounts.—Attempted mounts included all incidences of incorrect copulatory positions on females by male *C. mydas*, and all mounts of < 5 min. Mounts of <5 min were not included in the mounts category, because very short mounts generally do not involve intromission in these captive animals (Wood and Wood, 1980). Males occasionally mounted in reverse orientation or were unable to position themselves properly because the female was beached or was in water too shallow for mounting. Female beaching was noted by both Booth and Peters (1972) and Bustard (1973), and Bustard also described unsuccessful positioning of males on females. At the Cayman Turtle Farm, male *C. mydas* attempted to mount breeding females significantly more often than nonbreeding females (Table 1).

Mounts.—A male attached to a female by hooking his foreclaws on the anterior margin of her carapace and his rear flippers to the posterior margin of her carapace (cf. Booth and Peters, 1972; Bustard, 1973). A pair may remain mounted in this manner for up to 119 h (Wood and Wood, 1980). Because of the position of the male on the female, it is difficult to determine the extent of intromission and time of ejaculation during the mount. Statistical comparisons of the number of mounts of breeding and nonbreeding females were not made, because the mount data were used

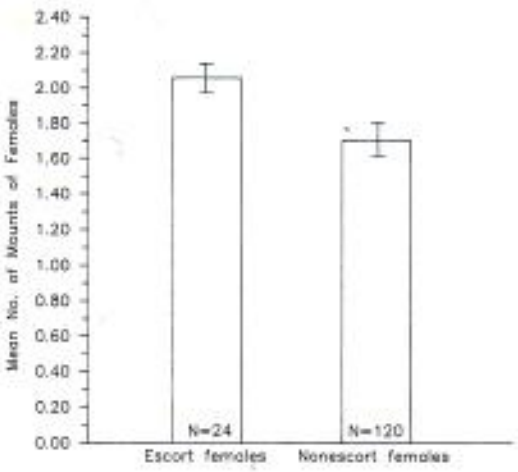

FIG. 2.—Mean frequencies of mounts of escort females and nonescort females, $t = 1.980$, $P < 0.05$, calculated using Student's t-test. Bars represent 1 SE.

to define the period of reproductive activity.

Copulation interference.—There are several accounts in the literature of mounted pairs being escorted by conspecific individuals or groups (Booth and Peters, 1972; Hendrickson, 1958; Hirth, 1971). The function of this behavior is unclear. At the turtle farm, mounted pairs were often accompanied by escort groups which were usually males, but sometimes included females. Escorting turtles bit the flippers or tail of the mounted male, and/or rammed their heads between the mounted pair's shells. Of 459 attempted and successful mounts, 114 (24.8%) were disrupted by interfering males and females. Of the 114, there were 21 (18.4%) subsequent attempted mounts of the female by a male from the escort group, but no subsequent successful mounts. The number of times a male escorted and the number of times he mounted over the entire season were positively correlated (Spearman's coefficient, $r_s = 0.430$, $t = 2.286$, 25 df, $P < 0.05$). Males escorted before, during, and after their own mating periods. Among breeding females, those that engaged in mount interference were subsequently mounted significantly more often than those that did not interfere with mounted pairs (Fig. 2). All females that interfered with mounted pairs did so before their day of maximum mating. In fact, 28 of the 32 (87.5%) instances of female interference occurred before the escorting female began her breeding period.

General Discussion

The data analyses suggest that the components observed at the Cayman Turtle Farm were specific to courtship, because males directed them at significantly higher frequencies to breeding females than to nonbreeding females. Females appeared to signal reproductive attractiveness by some mechanism, perhaps chemical, but then utilized mounting avoidance behaviors to allow the selection of specific males for mounting. Although the described components are based on observations of captive animals, we believe that they reflect behaviors found in wild populations.

We have observed biting, circling and biting, chasing, attempted mounts, and mounts in the wild in another study in Australia. These behaviors are qualitatively very similar to our observations at the Cayman Turtle Farm. Booth and Peters' (1972) descriptions of biting, circling and biting, chasing, mounting, and escorting also appear to be qualitatively similar, as are Bustard's (1973) descriptions of biting, chasing, attempted and successful mounting. All of these behaviors appear to be important parts of the natural courtship repertoire.

The first phase of courtship in *C. mydas* was determination of female reproductive status by the male. Although gular rubs and cloacal checks may provide tactile stimulation in preliminary courtship, they are also potential means by which conspecifics may assess a female's reproductive state. However, because breeding females were gular rubbed more often than nonbreeding females, it appears that their reproductive state had already been identified. Cloacal checks may represent chemosensory investigation of the approximate readiness of the female for mating. The presence of a chemical releaser (pheromone?) emanating from the cloaca has

been suggested in the freshwater turtle *Trachemys scripta* (Jackson and Davis, 1972*b*). Given the abilities of *C. mydas* to detect very minute quantities of a chemical (Manton et al., 1972*a*,*b*), a chemical signal released by the female could be detected by the male from far away, and used by him to locate the female. This would explain the ability of wild male *C. mydas* to find females experimentally tethered at night in murky water (C. Limpus, personal communication).

After breeding females had been detected, the next stages of courtship were the attempts by male *C. mydas* to properly position themselves for mounting. Females generally avoided mounting by biting, circling and biting, or swimming away (resulting in a chase). These behaviors may allow a female to exercise some control over which males mount her. The final stage of reproductive behavior was mounting (and intromission).

Although males participating in escorting groups were unsuccessful at mounting displaced females, mounting and escorting were positively correlated. Evaluated over an entire season, males that escorted more frequently also mounted more frequently. Escorting may increase a male's relative reproductive success not only by lowering the reproductive successes of the mounting males, but also by increasing his own opportunities for mounting at a later time. Male escorting, unlike female escorting, did not appear to be a precursor to mounting.

Escorting females that disrupted mounts were not subsequently mounted. Therefore, it is doubtful that the function of female escorting was to secure a mate for an imminent copulation. However, some advantage seems to be conferred by escorting, because females that escorted were mounted more than females that did not escort. Because females generally escorted before they began their breeding period, perhaps the function of female escorting was to decrease the likelihood of insemination of other females, which would in turn increase the amount of male resources available to the escorting females at a later time.

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