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LEPIDOCHELYS OLIVACEA

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Reproductive and Developmental Synchrony in Female Lepidochelys olivacea

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ABSTRACT.—The reproductive behavior and movements of arribada nesting olive ridley turtles (Lepidochelys olivacea) were studied during the 1990 and 1991 nesting seasons (September through November) at Nancite Beach, Santa Rosa National Park, Guanacaste, Costa Rica. Females that normally emerge synchronously once a month on Nancite Beach to oviposit delayed oviposition in response to a period of very heavy rainfall. Females retained oviducal eggs for 63 days and emerged synchronously to oviposit at Nancite Beach after the rain had ceased. Egg retention in L. olivacea appears to be an adaptation which enables delayed oviposition when environmental conditions are unsuitable and may also facilitate reproductive synchrony. We suggest that preovipositional arrest of developing embryos may have occurred while oviducal eggs were retained.

Marine turtles exhibit three distinct nesting emergence behaviors: solitary nesters individually emerge on beaches in the absence of or with few conspecifics (Carr et al., 1966), colonial nesters emerge individually and coincidentally with several to many conspecifics (Caldwell et al., 1959), and arribada nesters synchronously emerge en masse with hundreds to thousands of conspecifics (Pritchard, 1969). These mass emergences, referred to by the Spanish term arribada, occur in Mexico, Nicaragua, Panama, Costa Rica, India, and Surinam (Cornelius, 1986). With hundreds to thousands of turtles ascending a small area of beach within a few nights to lay eggs, arribadas are perhaps the most extraordinary examples of group coordinated behavior known for any reptile. For the olive ridley turtle (Lepidochelys olivacea), several arribadas generally occur each year during the nesting season, are temporally separated by two to four weeks (Pritchard, 1969), and occur only on specific beaches. Each arribada may last as long as seven consecutive nights during which several hundred thousand turtles may emerge to lay eggs (Pritchard, 1969; Cornelius, 1986; Dash and Kar, 1990).

Prior to an arribada, L. olivacea aggregate nearshore in front of the nesting beach (Cornelius, 1986; Plotkin et al., 1991). Some females emerge to oviposit before the arribada begins; however, the vast majority wait, presumably until the appropriate cues are present, before emerging en masse (Pritchard, 1969). The cues responsible for reproductive synchrony have long been subject to speculation by researchers. Winds, tidal cycle, lunar phase, rainfall patterns, temperature, photoperiod, physiological cues, and socially facilitated behavior have been suggested as potential regulators of arribada timing and occurrence (Pritchard, 1969; Owens et al., 1982; Mendonça and Pritchard, 1986; Cornelius 1986).

We investigated the reproductive behavior and movements of L. olivacea at Nancite Beach, Costa Rica during the nesting season. The purpose of this portion of the study was to investigate factors involved in reproductive synchrony of arribada nesting L. olivacea. Specifically we determined the impact of a period of heavy rainfall on nesting intensity, internesting interval, and retention of oviducal eggs by this species.

MATERIALS AND METHODS

Nancite Beach, located in Santa Rosa National Park, is in a remote area with very little human intrusion or disturbance. The beach, approximately 1 km in length, is bound on the north and south by two headlands, on the west by the Gulf of Papagayo, and on the east by a small valley of dry tropical forest. Both solitary and arribada nesting L. olivacea emerge on Nancite Beach throughout the year. However, most turtles nest during the largest arribadas which occur during the wet (rainy) season from July through December (Hughes and Richard, 1974; Cornelius, 1986). Arribada nesters exhibit site fidelity to Nancite Beach within a nesting season (Plotkin, 1994), oviposing only one or two egg clutches although three clutches rarely are observed (Cornelius, 1986; Plotkin, 1994). Arribada nesters exhibit site fidelity between nesting sea-
TABLE 1. Date and estimated number of *Lepidochelys olivacea* ovipositing during arribadas on Nancite Beach, Costa Rica, inter-arribada (IA) period* (days), lunar phase, and monthly rainfall totals (cm) for 1990 and 1991.

<table>
<thead>
<tr>
<th>Date of arribada</th>
<th>Estimated # turtles</th>
<th>IA period (days)</th>
<th>Lunar phase</th>
<th>Rain (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>13-14 Jul 1990</td>
<td>1090</td>
<td>—</td>
<td>last quarter moon + 2 d</td>
<td>1.11</td>
</tr>
<tr>
<td>11-12 Aug 1990</td>
<td>2300</td>
<td>28</td>
<td>last quarter moon - 2 d</td>
<td>5.11</td>
</tr>
<tr>
<td>17-22 Sep 1990</td>
<td>19,153</td>
<td>36</td>
<td>new moon</td>
<td>19.56</td>
</tr>
<tr>
<td>Oct 1990</td>
<td>—</td>
<td>NO ARIBADA OCCURRED</td>
<td>—</td>
<td>52.98</td>
</tr>
<tr>
<td>23-25 Nov 1990</td>
<td>14,580</td>
<td>62</td>
<td>first quarter moon</td>
<td>30.78</td>
</tr>
<tr>
<td>5-8 Aug 1991</td>
<td>2829</td>
<td>—</td>
<td>last quarter moon + 2 d</td>
<td>14.55</td>
</tr>
<tr>
<td>3-8 Sep 1991</td>
<td>16,869</td>
<td>26</td>
<td>last quarter moon + 2 d</td>
<td>19.18</td>
</tr>
<tr>
<td>1-4 Oct 1991</td>
<td>5622</td>
<td>23</td>
<td>last quarter moon</td>
<td>14.48</td>
</tr>
<tr>
<td>31 Oct-3 Nov 1991</td>
<td>17,069</td>
<td>27</td>
<td>last quarter moon</td>
<td>0.0</td>
</tr>
<tr>
<td>5-6 Dec 1991</td>
<td>1800</td>
<td>32</td>
<td>new moon</td>
<td></td>
</tr>
</tbody>
</table>

* Data for estimated number of turtles are from Gina Zanella, Carlos Calvo, and Claudette Mo, personal communication.

The number of turtles emerging on Nancite Beach was quantified daily from July through November 1990 and from August through December 1991. During arribadas the number of turtles nesting was estimated using a strip transect method (Cornelius and Robinson, 1986). Between arribadas, nightly beach surveys were conducted and visual counts were made of nesting turtles and/or their tracks. Turtles that emerged on the beach but did not oviposit before returning to sea were counted as non-nesters. We measured rain every day at midnight (12:00 AM) to the nearest mm with a rain gauge mounted on a wooden post in a clearing at the Nancite Beach Research Station located a few hundred meters behind the beach. Nearshore water temperature (approximately waist deep) was measured with a mercury thermometer and a water sample was collected and stored in screwtop glass jars approximately three times per week at 1200 h. The salinities of the water samples were measured later in the laboratory using an AGE salinometer.

In September 1990 and September 1991, we captured two groups of six turtles emerging on Nancite Beach at the same time and in close spatial proximity during arribadas. We examined the oviducts and ovaries of all turtles with an Aloka 500V ultrasound scanner with 5.0 MHz convex linear probe to assess their reproductive status (Rostal et al., 1990; Rostal, 1991). Following ultrasonography, approximately 15 ml of blood were collected from the cervical sinus of each turtle with a vacutainer or syringe (Owens and Ruiz, 1980). Blood samples were centrifuged and serum was pipetted into cryotubes and frozen in liquid nitrogen. Serum testosterone (T) concentrations, a known indicator of reproductive status in marine turtles (Wibbels, et al. 1990; Rostal, 1991), were measured later in the laboratory using radioimmunoassay procedures as described in Wibbels et al. (1990). Testosterone levels previously have been used successfully to indicate a marine turtle's stage in the reproductive cycle (i.e. first nesting, second nesting) (Wibbels et al., 1990; Rostal, 1991).

Satellite (UHF) transmitters (Telonics, Inc. model ST-3) were attached to 12 turtles possessing large numbers of vitellogenic follicles (>2 cm diameter) because these individuals were likely going to return to Nancite Beach that season to oviposit another egg clutch. Individual turtles were restrained by hand or tied to large plywood boards and a transmitter was attached with polyester resin and fiberglass cloth over the second neural scute. Turtles were held for approximately two to three hours until resin cured and then were released from the beach. Beach patrols were conducted nightly to recapture telemetered turtles returning to oviposit at Nancite Beach. Recaptured turtles were re-examined with ultrasonography, another blood sample was collected, and the turtles were released from the beach. Turtle movements were monitored via satellite until transmissions ceased or a transmitter was removed. Turtle locations (latitude and longitude) were calculated by Argos from doppler-shift in transmission frequency (Harris et al., 1990) and screened for errors (Plotkin, 1994).

**RESULTS**

In 1990, arribadas occurred once a month between the time just prior to last quarter moon and the new moon. There were two exceptions to this: the first occurred in October 1990 when there was no arribada and the second occurred in November 1990 when the arribada took place during first quarter moon (Table 1). The absence of the October 1990 arribada coincided with a temporale (Spanish term for a large storm system) that moved into the region in late September 1990. Rain fell at Nancite Beach daily from late September 1990 through early November...
1990, with the largest total monthly precipitation occurring in October (52.9 cm) (Table 1). Most of the rain (approximately 15 cm) occurred during the second week of October, just prior to the last quarter moon when we expected the arribada to commence, during the third week of October, when 24.8 cm of rain fell within 36 h, and during the first week of November when approximately 25.0 cm of rain fell over a 4 d period. Water temperature and salinity fluctuated throughout October, although the largest changes measured occurred in late October to early November. Water temperature nearshore decreased from between 29.0°C-30.0°C to 27.0°C in late October and in early November (1990 mean water temperature = 29.6°C, SD = 1.1, range = 27.0°C to 32.0°C). Salinity fluctuated between 30.29 ppt-33.35 ppt in October and experienced a precipitous decline to 27.18 ppt in early November (1990 mean water salinity = 32.34 ppt, SD = 1.19, range = 27.18 ppt to 33.50 ppt). The precipitation that fell during October 1990 saturated Nancite Beach, resulted in flash floods of local rivers, and caused a significant rise in and overflow of the estuary located behind Nancite Beach. The estuary broke through Nancite Beach at about its mid-point and created a temporary connection between the estuary and the Gulf of Papagayo. The rain ended at Nancite Beach in early November 1990 and the arribada occurred approximately two weeks later during first quarter moon, the only time nesting was observed during this moon phase (Table 1).

In 1991, arribadas occurred once a month, between the time just prior to last quarter moon and the new moon (Table 1). In contrast to 1990, rain was scarce during the 1991 nesting season at Nancite Beach. An El Niño, detected in the Pacific Ocean in late 1990 (Monastersky, 1993), altered weather patterns in 1991 and presumably was responsible for a drought that occurred in Costa Rica in 1991. Approximately 50.0 cm of rain fell at Nancite Beach between August and December 1991, less than half of what we recorded during the previous season.

The ovarian status and T levels of the turtles we attached transmitters to in September 1990 (Table 2) indicated they were going to oviposit another egg clutch during the nesting season and telemetry data indicated they were in or close to the Gulf of Papagayo during October 1990 (Plotkin et al., 1995). Contrary to our expectations however, an arribada did not occur in October 1990 and none of our telemetered turtles returned to oviposit at Nancite Beach during this month. The geographic locations and surface-submergence data we received for these turtles indicated that they did not nest elsewhere during this time period (Plotkin, 1994; Plotkin et al., 1995). The turtles later returned to Nancite Beach in November 1990, 66 d following their initial capture (Table 2) and five of the six were recaptured nesting during the arribada. Assuming that the turtles ovulated within 36 h after oviposition in September 1990 (Licht et al., 1982) and that egg calcification occurred within 72 h (Owens, 1980; Miller, 1985), and knowing that the turtles did not oviposit until 66 d after their initial capture, the minimum time that oviducal eggs were retained was 63 d.

Using ultrasonography in the field, we had some difficulty accurately determining ovarian status in several of the turtles we captured during the September 1991 arribada. Subsequent measurement of T levels verified that only three of the six turtles (turtles 83, 87, 89) we had attached transmitters to during the September 1991 arribada were gravid and could have oviposited another egg clutch during the nesting season. Satellite telemetry data showed that the three turtles with low T levels departed the Gulf of Papagayo and began postnesting migrations (Plotkin et al., 1995). The three turtles with high

### Table 2. Date of capture and recapture of female Lepidochelys olivacea, serum testosterone level (T) (pg/ml) and ovarian status (OS) (G = gravid, D = depleted) at capture and recapture, and duration of the internesting period (IP).

<table>
<thead>
<tr>
<th>Turtle #</th>
<th>Date captured</th>
<th>T</th>
<th>OS</th>
<th>Date recaptured</th>
<th>T</th>
<th>OS</th>
<th>IP (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>68</td>
<td>18 Sep 1990</td>
<td>192.8</td>
<td>G</td>
<td>24 Nov 90</td>
<td>16.7</td>
<td>D</td>
<td>66</td>
</tr>
<tr>
<td>69</td>
<td>19 Sep 1990</td>
<td>102.9</td>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>70</td>
<td>19 Sep 1990</td>
<td>187.6</td>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>71</td>
<td>19 Sep 1990</td>
<td>205.8</td>
<td>G</td>
<td>24 Nov 90</td>
<td>3.2</td>
<td>D</td>
<td>66</td>
</tr>
<tr>
<td>72</td>
<td>19 Sep 1990</td>
<td>224.3</td>
<td>G</td>
<td>24 Nov 90</td>
<td>5.2</td>
<td>D</td>
<td>66</td>
</tr>
<tr>
<td>73</td>
<td>19 Sep 1990</td>
<td>299.6</td>
<td>G</td>
<td>24 Nov 90</td>
<td>11.7</td>
<td>D</td>
<td>66</td>
</tr>
<tr>
<td>80</td>
<td>5 Sep 1991</td>
<td>362.5</td>
<td>G</td>
<td>3 Oct 91</td>
<td>3.2</td>
<td>D</td>
<td>28</td>
</tr>
<tr>
<td>83</td>
<td>5 Sep 1991</td>
<td>4.9</td>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>86</td>
<td>4 Sep 1991</td>
<td>246.9</td>
<td>G</td>
<td>1 Oct 91</td>
<td>21.5</td>
<td>D</td>
<td>28</td>
</tr>
<tr>
<td>87</td>
<td>5 Sep 1991</td>
<td>9.3</td>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>88</td>
<td>5 Sep 1991</td>
<td>140.7</td>
<td>G</td>
<td>2 Oct 91</td>
<td>15.3</td>
<td>D</td>
<td>29</td>
</tr>
<tr>
<td>89</td>
<td>5 Sep 1991</td>
<td>27.0</td>
<td>G</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
T levels stayed in the Gulf of Papagayo during the internesting period, returned to oviposit on Nancite Beach the following month, and were recaptured nesting during the October 1991 arribada, 28 and 29 d following their initial capture (Table 2).

**DISCUSSION**

Pritchard (1969) suggested that the synchronous emergence of gravid *L. olivacea* requires that either the eggs develop in all of the turtles in such perfect synchrony that the need to oviposit occurs simultaneously or that eggs develop at approximately the same time and the turtles retain their eggs until the appropriate cues bring about independent simultaneous oviposition. The delayed oviposition by *L. olivacea* that we observed at Nancite Beach in October 1990, and the lack of spatial association among our transmitted turtles during the internesting period (Plotkin et al., 1995) supports Pritchard's contention that the eggs develop at about the same time and are retained until turtles independently react and then oviposit simultaneously.

Oviducal egg retention has been described in freshwater and terrestrial turtles (Alho and Padua, 1982; see Buhlmann et al., 1995 for review) and is generally known to occur in marine turtles as well. Short term egg retention by marine turtles often occurs when females emerge on beaches to oviposit, are confronted with anthropogenic or natural disturbances, and then abort their nesting attempt and return to the sea. The turtles retain their eggs and later return to the beach to oviposit from one to a few days after their initial emergence. Long term egg retention has not been reported previously in marine turtles and appears to be unique to the genus *Lepidochelys*. *Lepidochelys olivacea* and its cogener Kemp's ridley (*L. kempi*) have internesting periods that may range from 14-75 d, with the average internesting period being approximately 28 d (Pritchard, 1969; Cornelius, 1986; Dash and Kar, 1990). All other marine turtle species have a significantly shorter internesting period that ranges from approximately 9-15 d (Ehrhart, 1982). These differences in internesting periodicity are not due to interspecific differences in ovulatory cycles. A comparison of the nesting and ovulatory cycles of *L. olivacea* that nested every 28 d with green turtles (*Chelonia mydas*) that nested every 14 d revealed that the time of ovulation relative to oviposition was similar for both species. Licht et al. (1982) concluded that the only difference between the two species was that *L. olivacea* was capable of retaining oviducal eggs longer.

Egg retention is believed to be an adaptation which facilitates postponement of nesting when unexpected changes in environmental conditions occur and nest sites become unavailable or unsuitable (Ewert, 1985). Nest sites were available for the *L. olivacea* that delayed emergence and oviposition at Nancite Beach in October 1990, but the sites may have been unsuitable. Excessive rainfall from temporales may compromise offspring survival. Normal levels of rainfall do not adversely impact the survival of postovipositional *L. olivacea* eggs buried in the sand on Nancite Beach, otherwise selection pressures would not have favored the timing of the nesting season to coincide with the rainy season. However, excessive rainfall, which is unpredictable but not uncommon in Costa Rica, may adversely affect the survival of postovipositional eggs (Ragotzkie, 1959; Kraemer and Bell, 1980). High sand moisture content can reduce hatching success by inhibiting or reducing gas exchange between the egg clutch and its surroundings (Packard et al., 1977; McGehee, 1990) or by promoting fungal growth on the eggshell (McGehee, 1990).

Egg retention may also be an adaptation that facilitates reproductive and developmental synchrony in aggregate nesting species. If the cue(s) that initiate a mass emergence is absent or altered, then egg retention provides the means by which the entire group can synchronously delay oviposition. In addition to the arribada nesting *L. olivacea*, the Amazon River turtle (*Podocnemis expansa*), another aggregate nesting turtle, also postpones nesting and retains oviducal eggs when environmental conditions are unsuitable (Alho and Padua 1982). Alho and Padua (1982) reported an instance when *P. expansa* already had started to emerge on shore en masse, ceased nesting when a sudden rise in waters covered most of the available nest sites, retained oviducal eggs, and then returned to the river. Five days later when water levels subsided the turtles returned to shore and synchronous nesting resumed.

The extended oviducal egg retention by the *L. olivacea* we monitored in 1990 suggests that either embryonic development was delayed during this time or that embryos continued developing. Because marine turtle eggs develop to the stage of middle gastrulation in the oviducts and cease development at this stage until after oviposition (Miller 1985), it is probable that embryonic development was delayed in the *L. olivacea* we monitored. Unfortunately, we did not open any of the retained eggs after they were oviposited to verify that embryo development indeed had been delayed. We also did not monitor the retained egg clutches during the incubation period to determine if they developed at a different rate compared to eggs that were retained in oviducts for a shorter time period. De-
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LITERATURE CITED


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