

## Nesting Ecology of the Leatherback Turtle, *Dermochelys coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica: 1988–1989 to 1999–2000

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We collected data on nesting ecology and identified individual turtles that nested at Parque Nacional Las Baulas, Costa Rica, one of the few remaining nesting sites for Pacific leatherbacks, from 1988–1989 to 1999–2000. We tagged individual female turtles with flipper tags and later with Passive Integrated Transponder (PIT) tags that permitted permanent identification. During the full calendar years of 1990 and 1995, over 93% of nests were laid between the beginning of October and the end of February. We found that  $92.4 \pm 1\%$  of nesting attempts resulted in successful oviposition, with a mean clutch size of  $64.7 \pm 1.4$  yolked and  $38.5 \pm 1.0$  yokless eggs ( $n = 1389$ ). Mean standard curved carapace length and curved carapace width during the surveyed years ranged from  $144.4 \pm 0.6$  cm to  $147.6 \pm 0.3$  cm and from  $103.9 \pm 0.3$  cm to  $105.5 \pm 0.6$  cm, respectively. Reproductive output as determined by estimated clutch frequency (ECF) ranged from  $4.3 \pm 0.2$  to  $7.9 \pm 0.3$  clutches per female per nesting season. The mean period between nesting seasons for an individual turtle was  $3.7 \pm 0.2$  years; only 15% of turtles tagged in 1993/1994 returned to nest again within six years. The nesting population declined from 1367 adult females in 1988/1989 to 231 in 1999/2000. The decline in the nesting population was apparently because of the low incidence of turtles returning to nest in more than one season.

THE leatherback turtle, *Dermochelys coriacea*, is among the largest reptiles (1000 kg) and is the most widely distributed sea turtle, ranging through all of the oceans except for the Arctic and Antarctic. Although large body size, effective insulation, and control of blood flow (a suite of adaptations termed gigantothermy) allow leatherbacks to inhabit cold water and dive to great depths (Paladino et al., 1990; Morreale et al., 1996), nesting activity is restricted to tropical and subtropical regions.

The leatherback is the sole member of the family Dermochelyidae and exhibits striking morphological and physiological differences from other living sea turtles that are all in the family Cheloniidae, having diverged about 100 million years ago (Pritchard, 1997). Apart from its large size, the most obvious morphological difference between leatherbacks and other sea turtles is the shell, which is composed of thousands of small, polygonal bones covered by a black, flexible skin with a leathery appearance (Wood et al., 1996). The flesh and skeleton are particularly oily, and for this reason leatherbacks have only been used as food by a few societies. The oil is more often sought after, and the eggs are highly prized as a food source and aphrodisiac (Lutcavage et al., 1997). The most obvious difference physiologically is their ther-

moregulatory ability via gigantothermy and their very rapid growth rate. Leatherback females mature in from five to 13 years, with the mean for a population around nine years (Zug and Parham, 1996).

Pritchard (1982, 1997) considered leatherbacks to be one of the most abundant sea turtles, but since then, populations in the Pacific Ocean and elsewhere have declined precipitously (Spotila et al., 1996). Populations in Malaysia have been extirpated, and those in Mexico and Costa Rica have decreased exponentially in the 1990s (Chan and Liew, 1996; Eckert, 1997; Spotila et al., 2000). Declines have been associated with egg harvesting, incidental capture in fisheries, and killing of adult turtles on the nesting beach (Pritchard, 1982). Recent analysis indicates that leatherbacks in the Pacific Ocean are in danger of extinction caused by high rates of mortality of adults at sea, apparently because of capture in fisheries (Spotila et al., 2000).

It is difficult to obtain data on leatherbacks at sea because they are seldom seen and rarely aggregate in defined feeding areas. Instead, they generally move throughout the oceans searching for areas such as upwellings that are rich in their prey of jellyfish, ctenophores, and other gelatinous zooplankton (Boulon et al.,

1988; Morreale et al., 1996). Thus, there is little opportunity to study juvenile or male turtles or the ecology of nonreproductive females, as there has been with other species (e.g., Carr, 1980; Bjørndal, 1997).

Our understanding of leatherback biology and ecology is obtained almost entirely through studies of nesting female turtles. Leatherback turtles are iteroparous and nest primarily during the dry season. Thus, leatherbacks on the Caribbean coast of Costa Rica nest mainly from March to July, whereas those on the Pacific coast nest from October to February. In both locations, some nesting occurs throughout the year. In general, females lay from four to eight nests in a season (Tucker and Frazer, 1991; Steyermark et al., 1996; Fretey and Girondot, 1998), once every nine days (Steyermark et al., 1996) and return to nest again (remigrate) in two to seven years, with a mean of three years (Boulon et al., 1996; Hughes, 1996). Nesting involves the same stereotyped behavior as that of other sea turtles (Carr, 1952). Between successive nests, leatherback females ovulate and deposit albumen and shell on about 65 eggs, with the reproductive cycle regulated by circulating levels of estrogen and progesterone (Rostal et al., 1996; Rostal et al., 2001).

Leatherbacks are long-lived, spending at least 20 years as breeding adults (Boulon et al., 1996; Hughes, 1996). Like other long-lived animals, they can only maintain viable populations if adult mortality remains low and adults return to nest over several years (Congdon and van Lobens Sels, 1993; Congdon and Gibbons, 1996; Spotila et al., 1996). Our ability to accurately measure the status of leatherback populations and to understand their population biology is tied to our ability to accurately count the number of nesting females in a population, to determine how often these females return to a given beach to nest within and between seasons, to measure the mean internesting period for each female, and to measure the reproductive success of individual turtles (Meylan, 1982; Congdon and Gibbons, 1996). In the past, it was rarely possible to record the complete nesting activity of every female in any but the smallest populations. However, by identifying every individual in the nesting population with passive integrated transponder (PIT) tags and by maintaining 90–95% beach coverage throughout the main nesting season, we have been able to get these kinds of data for the leatherback turtle population at Parque Nacional Marino Las Baulas in Guanacaste, Costa Rica.

Despite the exponential decline since 1990 (Spotila et al., 2000), the beaches at Las Baulas

still support the largest nesting population of leatherbacks on any single beach complex in the Pacific Ocean. Described by Steyermark et al. (1996), the Park encompasses three nesting beaches totaling 5.8 km. Leatherbacks nest primarily on the central beach of Playa Grande, and here we report 12 years of data on nesting leatherbacks from that beach. Accurate measurements of nesting parameters and identification of individual turtles allowed us to determine population size, remigration rates of turtles tagged in previous seasons, effect of tide cycle on emergence, reproductive frequency, internesting period, and reproductive output for this population. By combining the results of detailed data collection since 1994–1995 with a reanalysis of population estimates from nest surveys from 1988–1989 to 1993–1994 we have generated an accurate picture of the changes in the population through this time.

#### MATERIALS AND METHODS

We conducted tagging surveys and collected nesting data at beaches in Parque Nacional Las Baulas ("Las Baulas") as described previously (Steyermark et al., 1996). During the nesting season, we took nightly counts of body pits made by turtles as they nested or attempted to nest, tagged individual turtles with PIT tags, recorded dates and times of nesting activity, and measured individual females. We counted fresh body pits at dawn, when they were most easily discerned. In 1990 and 1995, body pits were counted during the entire calendar year. We applied iconel flipper tags (National Band and Tag Co., Style 681) to the skin of the rear flippers until 1996–1997 (Steyermark et al., 1996) and since 1993/1994 injected PIT tags into the muscle of both left and right shoulders using standard techniques (Dutton and McDonald, 1994; Steyermark et al., 1996). We tagged and identified turtles using hand-held PIT tag scanners (AVID Marketing) during egg laying or shortly after while turtles were covering their nest. We recorded successful or aborted nesting activity of each turtle after the visual observation of oviposition or the observed failure of the turtle to lay. We classified a nest as unknown if oviposition was not observed. We counted eggs as they were laid and distinguished yolked and yolkless egg types by their visibly large size difference (Hirth, 1980). We measured carapace length and width  $\pm 0.5$  cm (Steyermark et al., 1996) as turtles were laying their eggs or were motionless after laying. Standard curved carapace length (SCCL) was measured from the center of the nuchal notch along the side of the

dorsal ridge, to the tip of the carapace (caudal peduncle). Curved carapace width (CCW) was measured from the widest point of the most lateral ridge (4th longitudinal) over the carapace to the most lateral ridge on the other side.

From the recorded nesting data, we calculated several parameters based on observed or inferred nesting activity. Oviposition was confirmed if we observed eggs, or it was inferred when we did not observe eggs, provided that the individual turtle was not identified in a similar, unverified nesting attempt in the six days before or six days after the inferred oviposition. An interval of six days or less is not sufficient for ovulation and full formation of eggshell for a new clutch of eggs (Rostal et al., 1996; Miller, 1997), and thus two separate nesting events cannot take place within that time. We classified unverified nesting attempts as an aborted nest if we observed the turtle successfully nesting in the subsequent six days. The mean Observed Internesting Period (OIP) was calculated from the number of days between observed or inferred ovipositions by an individual female. We excluded data where the interval was 14 days or greater because the turtle could have nested twice during this time based on the six-day minimum interesting interval determined by Miller (1997). Observed Clutch Frequency (OCF) was the number of observed or inferred clutches laid by an individual female during a season, but OCF was dependent on census effort and underestimated actual nesting effort unless every turtle was encountered on every nesting occasion. Therefore, we determined the Estimated Clutch Frequency (ECF) from the first and last appearance dates for an individual using the mean interesting period to calculate the number of clutches of eggs that the female would have laid during that time and adding 1 for the first oviposition. The ECF is a more accurate estimate of nesting activity because the calculation includes unobserved nestings. Beach coverage was used as a measure of the census effort and was determined as the percentage of all nesting attempts where the individual female was observed and identified. Our techniques for measuring and calculating these parameters followed those of Steyermark et al. (1996) except for the criteria for the determination of observed or inferred successful nesting activity, thereby reducing the possibility of including aborted nests in this category. Aborted nests were indistinguishable from successful nests if observed after the turtle covered the nest. We analyzed the data of Steyermark et al. (1996) on unverified nesting attempts using these criteria

and recalculated the nesting parameters listed above.

For years when tagging surveys were conducted (1993–1994 to 1999–2000), we determined the total number of females during the survey period by the sum of identified (tagged) and unidentified (untagged) individuals. Unidentified turtles were turtles that nested but that we never tagged. We estimated the number of unidentified turtles for a given survey period by calculating the probability that a turtle was missed on every occasion that it nested, based on beach coverage (determined from all observed and unobserved nests) and ECF for that season. We used the following equation:  $N = [(U \times S) (1 - B)^{ECF}]$ , where  $N$  = number of unidentified turtles,  $U$  = number of body pits for which the turtle was unknown,  $S$  = decimal fraction of successful nesting attempts, and  $B$  = decimal fraction beach coverage. The number of unidentified turtles is thereby determined as a function of the number of times they are likely to have nested and the efficiency of beach patrols.

When only body pits were recorded (1988–1989 to 1992–1993), we determined the mean proportion of body pits, which resulted from a successful nesting (based on the percentage of known aborted nesting attempts from 1993–1994 to 1999–2000) multiplied by the number of body pits counted and divided by ECF to estimate the number of individual females.

We determined turtle numbers for a given nesting year by taking the number of turtles counted during the nesting season and comparing that to the distribution of nesting activity over the year found on the two full-year surveys in 1990 and 1995, because turtles that nested from March to October were not counted in our surveys. We determined the temporal distribution for the year and recalculated turtle numbers during the periods surveyed in each year to obtain a total number of turtles for the full nesting year. This number was always higher than the number we actually counted because it included all turtles for the year rather than a subset.

We calculated mean remigration rate and mean remigration interval for individual turtles that we observed nesting in more than one season. The proportions of new and remigrant turtles in a particular year were calculated in the same manner. A new turtle was one that was untagged, whereas a remigrant turtle was one that returned to nest in a year subsequent to the one in which we originally tagged it (Miller, 1997). Thus, after 1993–1994, we observed both

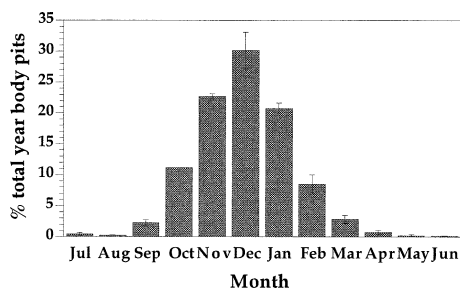


Fig. 1. Monthly distribution of leatherback turtles nesting at Playa Grande and Playa Ventanas in Parque Nacional Las Baulas, Costa Rica from full-year body pit counts in 1990 and 1995. Bars show mean  $\pm$  1 SE.

new turtles that were untagged and remigrant turtles that had been tagged in a previous year.

A one-way analysis of variance determined whether size differences between turtles of different nesting seasons and differences in nest frequency and clutch size between seasons (Sokal and Rohlf, 1981) were statistically significant. Regression analysis determined relationships between nesting parameters (OCF and ECF) and survey parameters (length of survey period and beach coverage). In all cases significance was assumed at  $P < 0.05$ .

## RESULTS

*Temporal distribution of nesting activity.*—In 1990 and 1995, turtles laid  $93.3 \pm 1.6\%$  of nests between the beginning of October and the end of February (Fig. 1). Nesting in May to August accounted for only about 1% of the year's total.

*Nesting status.*—Of observed nesting attempts at Playa Grande between 1993–1994 and 1999–2000,  $92.4 \pm 1.0\%$  ( $n = 6213$ ) resulted in successful oviposition,  $7.2 \pm 0.8\%$  of nests were aborted and  $0.4 \pm 0.2\%$  contained only yolkless eggs. Turtles aborted nests because of dry or unsuitable sand conditions, disturbance by other turtles, human interference or other reasons that were not apparent. Mean clutch size was  $64.1 \pm 1.4$  yolked and  $38.5 \pm 1.0$  yolkless eggs ( $n = 1389$ ). Body pit totals for each year included both observed and unobserved nesting (Table 1).

*Carapace measurements.*—We measured over 75% of turtles three or more times during the season and used the mean measurement in subsequent calculations. The range of Standard Curved Carapace Length (SCCL) was from 123–170 cm and the range for Curved Carapace Width (CCW) was from 94–118 cm, length and width

were significantly related ( $SCCL = 11.57 + 1.28 \times CCW$ ,  $P < 0.01$ ,  $R^2 = 0.985$ ,  $n = 1765$ ). There was no significant difference in mean SCCL or CCW between nesting seasons (Table 1). There were no significant relationships between carapace size (both SCCL and CCW) and Estimated Clutch Frequency (ECF) or number of yolked or yolkless eggs laid.

*Times of nesting activity.*—The time of turtle nesting activity was loosely associated with the time of the high tide (Fig. 2). After sunset, turtles typically emerged prior to the high tide and continued to emerge for up to 4 h after peak high tide. The timing changed with the tidal cycle; on nights where both afternoon and morning high tide occurred within about 2 h of darkness, turtles emerged all through the night, regardless of tide position.

*Duration of nesting process.*—The mean time taken for nesting turtles to dig a body pit was  $16.5 \pm 0.8$  min ( $n = 82$ ), to dig the nest cavity was  $17.4 \pm 0.7$  min ( $n = 147$ ), to lay eggs was  $12.7 \pm 0.4$  min ( $n = 164$ ), and to cover the nest was  $47.3 \pm 3.6$  min ( $n = 173$ ). The total nesting duration was  $117.8 \pm 17.5$  min (range 83 min to 187 min,  $n = 84$ ) with the measured time taken to crawl to the nest site and later to return to the ocean ranging from 7 min to 65 min each direction (mean = 22 min) as the position of the waterline changed relative to the nest.

*Observed and estimated clutch frequency.*—Observed (OCF) and estimated clutch frequencies (ECF) varied from year to year (Table 2). Both mean OCF and mean ECF were positively correlated with length of survey period ( $P < 0.01$ ,  $R^2 = 0.868$  and  $P < 0.05$ ,  $R^2 = 0.638$ , respectively) and beach coverage ( $P < 0.05$ ,  $R^2 = 0.806$  and  $P < 0.05$ ,  $R^2 = 0.621$ , respectively). The maximum OCF was 13 clutches for an individual female turtle in 1996–1997 and the maximum ECF was 14 clutches in 1998–1999. The ECF was typically bimodal at six and nine clutches.

We recalculated ECF for years with the longest survey period (1996–1997 to 1999–2000) by excluding turtles that were first observed before 15 October or after 15 December each year. If a turtle had not been observed attempting to nest in the 14 days after commencement of data collection, we presumed that the first observation after 15 October was its first nesting attempt. We calculated that the mean length of the nesting season for an individual turtle was approximately 60 days and so selected 15 December as being approximately 60 days prior to

TABLE 1. SUMMARY OF NESTING DATA, CARAPACE MEASUREMENTS, AND EGG NUMBERS FOR LEATHERBACK TURTLES AT PARQUE NACIONAL LAS BAULAS SINCE 1988. FROM 1988–1989 TO 1992–1993 THE BODY PIT COUNTS ON PLAYA GRANDE AND PLAYA VENTANAS WERE NOT RECORDED SEPARATELY. CARAPACE MEASUREMENTS AND EGG COUNTS PER CLUTCH ARE SHOWN AS THE MEAN ± 1 STANDARD ERROR. GRAN. IS PLAYA GRANDE, VENT. IS PLAYA VENTANAS, LANG. IS PLAYA LANGOSTA, SCCL IS STANDARD CURVED CARAPACE LENGTH, CCW IS CURVED CARAPACE LENGTH.

Survey dates	Body Pits			Measurements (cm)				Eggs	
	Gran.	Vent.	Lang.	SCCL	CCW	Yolked	Yolkless		
1/11/88–15/2/89	7409	390							
1/11/89–15/2/90	7243	405							
1/11/90–15/2/91	3615	182							
1/11/91–15/2/92	4218	174				65.3 ± 2.3		39.4 ± 3.2	n = 48
1/11/92–15/2/93	4976	211							
1/11/93–27/2/94	605	20		144.4 ± 0.6	103.9 ± 0.4				n = 156
29/10/94–23/2/95	1548	90	1196	147.6 ± 0.3	105.3 ± 0.2				n = 425
30/10/95–20/2/96	1116	72		145.7 ± 0.4	104.7 ± 0.3				n = 310
10/10/96–19/2/97	655	16	125	145.8 ± 0.6	104.2 ± 0.4				n = 114
28/9/97–16/2/98	1036	96	446	145.1 ± 0.4	103.9 ± 0.3				n = 201
28/9/98–24/2/99	743	23	50	146.4 ± 0.5	105.5 ± 0.5				n = 177
1/10/99–17/2/00	1220	19		147.0 ± 0.3	105.6 ± 0.3				n = 382
						58.9 ± 1.9		40.5 ± 2.0	n = 74
						65.9 ± 1.0		39.2 ± 0.9	n = 311
						66.9 ± 1.3		36.1 ± 1.1	n = 192
						67.5 ± 0.7		39.0 ± 0.8	n = 394
						62.8 ± 1.2		41.6 ± 1.1	n = 236
						61.5 ± 1.5		33.5 ± 1.4	n = 134



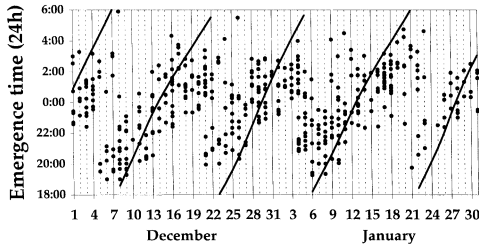


Fig. 2. Representative data on emergence of nesting leatherback turtles at Playa Grande from December 1998 and January 1999 showing the time of observed turtle activity (solid black circles) and time of the high tide each night (black line). The high tide advances between 40 and 60 min per day dependent on the phase of the lunar cycle.

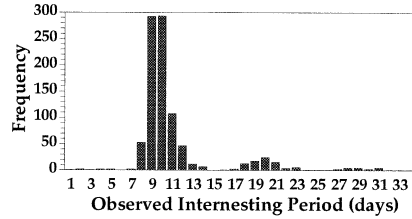


Fig. 3. Frequency distribution of the Observed Internesting Period (OIP) for leatherback turtles at Playa Grande during the 1997–1998 season.

the end of our survey period. We, thereby, avoided the possibility of underestimating ECF because a turtle commenced its nesting season before we began surveys or because it did not finish until after we ended. Using these criteria, the mean ECF values for the 1996–1997, 1997–1998, 1998–1999, and 1999–2000 seasons were  $7.9 \pm 0.3$  ( $n = 86$ ),  $6.4 \pm 0.3$  ( $n = 125$ ),  $6.9 \pm 0.4$  ( $n = 64$ ), and  $7.4 \pm 0.2$  ( $n = 124$ ) clutches per female, respectively.

*Observed internesting period.*—The mode of OIP distribution was at nine days, with smaller peaks visible at 18 and 27 days (Fig. 3). Mean OIP differed slightly but not significantly from year to year (Table 2). Mean OIP from 1993–1994 to 1999–2000 was  $9.5 \pm 0.04$  days ( $n = 3683$ ). We excluded OIP values less than seven or greater than 14 days as either aborted nesting attempts

or as including an unobserved nesting (Rostal et al., 1996; Steyermark et al., 1996; Miller, 1997).

*Interseasonal return rates and interval.*—From 1993–1994 to 1999–2000, we PIT tagged 1349 female leatherbacks, of which 207 remigrated to nest in a later season (Table 3). Only 15.2% of turtles tagged in 1993–1994 returned in the subsequent six years, and 26.0% of turtles tagged in 1994–1995 returned in the subsequent five years. Mean remigration interval increased each year as more tagged turtles returned and in 1999–2000 was  $3.7 \pm 0.2$  years ( $n = 92$ ). Most turtles returned in the third year, representing 35% of turtles that returned and 5.3% of all turtles tagged. However, only turtles tagged before 1996–1997 had sufficient time to return with a remigration interval of three years or greater.

*Amount of nesting activity and number of nesting females.*—The amount of nesting activity as determined by body pits counted on Playa Grande

TABLE 2. OBSERVED CLUTCH FREQUENCY (OCF), OBSERVED INTERNESTING PERIOD (OIP), ESTIMATED CLUTCH FREQUENCY (ECF), AND BEACH COVERAGE (PERCENTAGE OF NESTING ATTEMPTS WHEN THE TURTLE WAS IDENTIFIED) OF LEATHERBACK TURTLES AT PLAYA GRANDE FROM 1993–1994 TO 1999–2000.

Survey dates	Days surveyed	OCF (no. of nests)	OIP (days)	ECF (no. of nests)	Coverage (%)
1/11/93–27/2/94	116	$4.0 \pm 0.2$ $n = 146$	$9.5 \pm 0.1$ $n = 290$	$5.5 \pm 0.3$ $n = 146$	65
29/10/94–23/2/95	117	$3.7 \pm 0.1$ $n = 412$	$9.3 \pm 0.1$ $n = 801$	$4.9 \pm 0.1$ $n = 412$	68
30/10/95–20/2/96	112	$3.2 \pm 0.1$ $n = 322$	$9.4 \pm 0.1$ $n = 563$	$4.3 \pm 0.2$ $n = 322$	51
10/10/96–19/2/97	132	$5.2 \pm 0.3$ $n = 109$	$9.5 \pm 0.1$ $n = 462$	$6.0 \pm 0.3$ $n = 109$	80
28/9/97–16/2/98	140	$4.8 \pm 0.2$ $n = 175$	$9.3 \pm 0.1$ $n = 841$	$5.4 \pm 0.2$ $n = 175$	90
28/9/98–24/2/99	148	$5.6 \pm 0.3$ $n = 108$	$9.6 \pm 0.1$ $n = 434$	$6.4 \pm 0.3$ $n = 108$	87
1/10/99–17/2/00	140	$5.2 \pm 0.2$ $n = 211$	$10.0 \pm 0.1$ $n = 292$	$7.0 \pm 0.2$ $n = 179$	85

TABLE 3. NUMBER OF LEATHERBACK TURTLES PIT TAGGED AND REMIGRANT TURTLES AT PLAYA GRANDE DURING THE FIELD SEASONS 1993–1994 TO 1999–2000. For each year, the number of turtles tagged is shown, as well as the number that returned in each subsequent year and the total for all years of data. The proportion of migrant turtles and the mean remigration interval for that survey year are shown.

Year tagged	Nested in 1993–1994	Nested in 1994–1995	Nested in 1995–1996	Nested in 1996–1997	Nested in 1997–1998	Nested in 1998–1999	Nested in 1999–2000	Total returned 1994–1995 to 1999–2000	Remigrants in year	Mean remigration interval (years)
1993–1994	151	0	2	6	6	4	5	23 (15.2%)	—	—
1994–1995	—	438	1	25	49	8	31	114 (26.0%)	0%	—
1995–1996	—	—	322	0	4	10	32	46 (14.3%)	0.9%	1.7
1996–1997	—	—	—	85	0	0	7	7 (8.0%)	26.7%	2.2
1997–1998	—	—	—	—	160	0	17	17 (11%)	26.9%	3.0
1998–1999	—	—	—	—	—	81	0	0 (0.0)	21.4%	3.0
1999–2000	—	—	—	—	—	—	112	—	45.1%	3.7
<b>Total</b>	151	438	325	116	218	107	204	207		

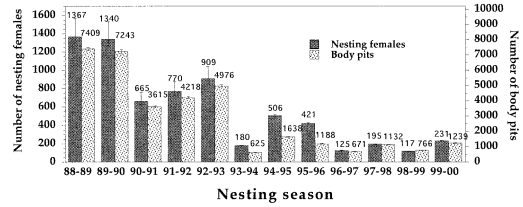


Fig. 4. Number of nesting female leatherbacks and number of body pits at Playa Grande, Costa Rica from 1988–1989 to 1999–2000. We calculated numbers from 1988–1989 to 1992–1993 from nest counts and an ECF of 6.8 clutches per female. Error bars show error of minimum and maximum ECF from 1996–1997 to 1999–2000 (ECF 6.4–7.9). We determined numbers from 1993–1994 to 1999–2000 from actual numbers of female turtles tagged during the survey period and calculated for the full year from temporal distribution of nesting activity. Error bars from 1993–1994 to 1999–2000 show error in calculation of full-year total from subset of data collected from October to March each season. Body pit count error was calculated in the same manner.

fell from 7409 body pits in 1988–1989 to 1239 body pits in 1999–2000 (Fig. 4). We recalculated historical numbers of turtles nesting based on these body pit count data and our new clutch frequency data. Turtles were not tagged in the years 1988–1989 to 1992–1993, so we estimated numbers of turtles from the number of body pits and the ECF. We calculated a historical ECF for these seasons of 6.8 clutches per female using the mean ECF of 7.2 clutches for turtles first observed between mid-October and mid-December for the 1996–1997 to 1999–2000 seasons with a 5% correction because of shorter length of the survey period. Turtle numbers for the 1993–1994 to 1999–2000 seasons were determined from actual number of turtles tagged during the survey period and extrapolated to the full year from our data on temporal distribution of turtle activity. We had confidence in the estimates of numbers of turtles for years 1988–1989 to 1992–1993 because, when we compared estimates for later years based on numbers of body pits and ECF, they were essentially the same as numbers of turtles actually tagged in those years. The number of nesting females declined from 1367 in 1988–1989 to 231 in 1999–2000 (Fig. 4). This decline has not been at a constant rate, ranging from an 80.2% decrease between the 1992–1993 and 1993–1994 seasons to a 181% increase between the 1993–1994 and 1994–1995 seasons. The inferred mortality rate for turtles with the longest possible time to return (1993–1994 and 1994–1995 seasons) was 25% annually.

*Nesting beach fidelity.*—From 1996–1997 to 1998–1999, we surveyed all three beaches of the national park and observed some turtles nesting on two or more beaches. Of the turtles that nested on Playa Grande in 1996–1997, 1997–1998, and 1998–1999, we observed 22.9%, 43.4%, and 10.2%, respectively, nesting on at least one of the other beaches in the national park. Beach coverage and the length of the survey period were not equal on all beaches; thus, it was not possible to determine the exact contribution of each beach to the total nesting activity in the park.

#### DISCUSSION

Parque Nacional Las Baulas is one of the few important nesting locations remaining for leatherback turtles in the Pacific. Of the three beaches in the park, Playa Grande has been the most important and the most intensively studied; hence, most comparative data are reported for this beach alone. Nesting activity on Playa Grande was approximately normally distributed through time, with 93% of nests laid during what is considered the nesting “season” from October to the end of February. The remaining 7% of nesting events took place over seven months. It is typical for sea turtles to show a peak of nesting activity in this way, coinciding with the arrival of migrating female turtles from a wide region (Miller, 1997). High densities of nesting per unit area occur during the peak of the season and may result in reduced success of oviposition or nest development because of interference of nesting females or disturbance of the nest by subsequently nesting turtles. This occurs in olive ridley turtles, *Lepidochelys olivacea* (Clusella, 2000), but although leatherbacks occasionally disturbed each other while nesting, at present nesting densities this does not appear to be a problem at Playa Grande (Reynolds, 2000).

Female turtles aborted about 7% of nesting attempts after they began digging a body pit. It is important to verify that individual nesting attempts are successful when basing population estimates on the level of nesting activity, or population size will be overestimated. Higher proportions of aborted nesting attempts occur on other beaches, up to a seasonal mean of 28% in Malaysia and the U.S. Virgin Islands (Chua and Furtado, 1988; Boulon et al., 1996). However, these reports did not define nesting attempts, whether it was emergence from the water or commencement of a body pit by the turtle, so their percentages may not be directly comparable to our data. It is most appropriate

to count body pits and determine nesting success as a proportion of body pits commenced, rather than on any other parameter of nesting activity. It is not possible to count all turtles that emerge from the water but return before crawling up the beach, and tracks are often washed away during the night, so counting body pits in the early morning is the most reliable estimate of total nesting activity on the beach. Some nests were aborted because the nest’s sides collapsed, and the success of nesting attempts will probably vary with the physical characteristics of the sand type. Hence, care must be used when applying data from one location to another.

Female leatherbacks nesting at Las Baulas are smaller than those nesting in other parts of the world, including Irian Jaya (Starbird and Suarez, 1994), South Africa (Hughes, 1996), Puerto Rico (Tucker and Frazer, 1991), French Guiana (Fretey and Girondot, 1988), and the Caribbean coast of Costa Rica (Hirth and Ogren, 1987; Leslie et al., 1996). The von Bertalanffy growth curve based on leatherback curved carapace length (SCCL; Zug and Parham, 1996) predicts the age of the smallest and largest turtles measured at Playa Grande to be about eight years and greater than 14 or 15 years, respectively, with a mean predicted age of the nesting population since 1993/1994 of about 12 to 13 years. However, the asymptote of the curve is between 147 cm and 148 cm SCCL, and it is difficult to predict with confidence the age of turtles larger than that size.

Significant relationships between carapace size and clutch size in sea turtles may (Frazer and Richardson, 1986; Hirth and Ogren, 1987) or may not (Tucker and Frazer, 1991) occur. We found no significant relationship between reproductive output and carapace length or width. Data must be collected on clutch size and frequency for individual turtles to determine these reproductive parameters.

The timing of turtle emergence and nesting activity was clearly related to tide cycles, with the majority of nesting activity taking place within a few hours of the high tide. At Playa Grande the vertical distance between low and high tide can reach 4 m, and the horizontal distance ranges from 50 m to over 100 m depending on the moon phase. Therefore, turtles have a clear advantage when emerging and returning to the water as close as possible to high tide. Turtles that emerged at low tide spent up to 65 min crawling across the intertidal sand flat before reaching the nest site. Although some returned to the water before reaching the beach, others continued and nested successfully. Turtles apparently vary nesting location and night of



emergence during the lunar month in response to changing hydrodynamic conditions (Fretey and Girondot, 1989b; Girondot and Fretey, 1996), but their pattern of nesting activity in relation to the tide on a given night has not been shown previously. At Tortuguero, on the Caribbean coast of Costa Rica, the tidal range is less than 1 m, and there is no apparent relationship between leatherback emergence and tidal cycle (Leslie et al., 1996).

The distance the turtle crawled from the water to the nest and back increased as they nested further in time from the high tide. The crawling phase of nesting behaviour varied more than the stationary phases (digging, laying, and covering). Unlike other turtles, leatherback turtles employ only a "swing-and-stance" gait, with all four limbs retracted and protracted simultaneously when crawling on sand. They are unable to lift the plastron clear of the sand surface, resulting in a slow, inefficient crawl (Wyneken, 1997).

The energetic consequence of distance between the nest location and the waterline can be seen when we consider our data on nesting duration and the measurements of oxygen consumption made by Paladino et al. (1996). During digging, laying, and resting phases, leatherback turtles consumed 2.87, 0.87, and 1.20 ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>, respectively. We calculate a mean oxygen requirement of about 215 ml O<sub>2</sub> kg<sup>-1</sup> during an average stationary nesting phase. Crawling on sand is slightly less demanding than digging and requires approximately 2.6 ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> (calculated from Paladino et al., 1990). Those turtles that nested at high tide spent about 15 min crawling and so required about 40 ml O<sub>2</sub> kg<sup>-1</sup> while doing so. Thus, 16% of their total oxygen consumption on land occurred while crawling to and from the nest site. In contrast, those turtles that nested at low tide spent up to 100 min or more crawling to and from the nest site and consumed up to 260 ml O<sub>2</sub> kg<sup>-1</sup> in the process or 55% of their total oxygen consumption while on land. Selection of emergence time by nesting females thus has a great effect on their oxygen requirement and hence the energetic cost of nesting.

The OIP varied little between nesting seasons with a mean and mode of 9.4 and 9.0 days, respectively. The short OIP interval, number of clutches laid during the season, and number of eggs laid per clutch mean that leatherbacks lay on average 450 eggs in each reproductive season, more than any other sea turtle (Miller, 1997) and apparently more than any other reptile (Porter, 1972).

The OCF and ECF are important indirect

measures of nesting activity, but they are highly sensitive to changes in survey timing and technique. We saw a gradual increase in OCF since 1993–1994, correlated with longer and more effective survey periods. OCF values are typically higher in smaller populations (Tucker and Frazer, 1991; Boulon et al., 1996) than in larger ones (Fretey and Girondot, 1989a, 1998), as a consequence of increased opportunity to encounter all nesting females on a given night. As survey length and beach coverage approach maximum, so OCF and ECF approach the true nesting frequency of leatherback turtles.

We used ECF as an approximation, but turtles that nested partially outside the survey period caused an underestimation of this parameter. We reduced this possibility by calculating ECF only from turtles that commenced nesting between 15 October and 15 December. The resulting ECF varied by nesting season (7.9–6.4 clutches) but was consistently higher than the ECF calculated from the entire survey period of the nesting season in question. The mean ECF obtained by this technique was 7.2 clutches per female, at the upper end of estimates calculated at Culebra, Puerto Rico (Tucker and Frazer, 1991), where a small colony nested on an intensively surveyed, small beach. The true mean biological clutch frequency is therefore most likely to be between seven and eight clutches per season, and a calculated ECF lower than seven is probably an artifact of survey period and intensity.

Calculation of ECF by this technique has not been employed previously, but it permits a more accurate assessment of nesting activity during surveyed periods. Thus, when we recalculated historical nesting data for 1988–1989 to 1992–1993, we applied the rate derived from the technique described above. When saturation tagging is not possible, the ECF can be used as an indirect measure, but accurate assessments of population size should be determined by mark-recapture data using permanent tags to identify individuals. Mark-recapture data of this type have been critical to the understanding the reproductive ecology of other long-lived species (Gibbons, 1969; Congdon and van Loben Sels, 1993; Congdon and Gibbons, 1996).

Playa Grande is the primary nesting beach in Parque Nacional Las Baulas, but the data on nesting beach fidelity from 1996–1997 to 1999–2000 showed that all three beaches in the park were used by the nesting population. Chaves et al. (1996) reported that up to 20% of turtles nesting on adjacent Playa Langosta also nested on Playa Grande in 1993–1994, although we were not able to quantify exchange rates in sub-

sequent years because of differences in the survey period on the different beaches. Other species of sea turtles show very high fidelity in returning to the beach from which they hatched (Lohmann et al., 1997), but it appears that leatherbacks show greater variation in selection of nesting beach than other sea turtles (Tucker and Frazer, 1991) and target a region of coastline rather than a specific beach. Such variation would ensure that nests are exposed to a variety of microenvironmental conditions and reduce the likelihood of losing all clutches to unfavourable conditions at a single location.

The return rate of tagged turtles was between 16% and 25% in the five or six years following the year of tagging. At St. Croix, U.S. Virgin Islands, about 60% of tagged turtles returned over the same period (McDonald and Dutton, 1996). Spotila et al. (2000) calculated a mean annual mortality rate of about 35% for the leatherbacks nesting at Las Baulas, predicted a fall to 50 nesting individuals by 2005–2006, and suggested that fishing industry practices in the Pacific were the cause of unsustainable adult mortality. An additional year of data lowered the estimate to 25%, but this rate still predicts extinction of this population in the relatively near future. Annual mortality rates are 4–10% for an apparently stable population nesting at St. Croix (Dutton et al., 1999).

The number of individual turtles nesting in a single season at Las Baulas fell almost 85% in 11 years. The amount of nesting activity determined from the number of body pits declined in parallel. The largest population decline was detected between the 1992–1993 and 1993–1994 seasons. Although this coincided with the introduction of the tagging program and a more direct measure of turtle numbers than the body pit count data used previously, this result was not an artifact of changing methodology. The methodology for counting body pits did not change, but the number of body pits fell almost 90% from 1992–1993 to 1993–1994. Leatherback nests on Playa Grande had been very heavily poached during most of the 1980s (Steyermark et al., 1996), and hatchling recruitment was correspondingly low. With a mean age at sexual maturity of the population of around nine or 10 years based on growth modeling (Zug and Parham, 1996), the effects of reduced recruitment would have been most obvious during the early 1990s, with few new adult females to replace those lost from the population. A similar pattern resulting in population extinction caused by uncontrolled poaching was seen in Malaysia over several decades (Chan and Liew, 1996). Although nest poaching has been

largely controlled since the early 1990s, the intensity of fishing activity in regions through which leatherbacks migrate has increased over the past 20 years (Eckert, 1997; Spotila et al., 2000) and has resulted in increased mortality rates for both new and remigrant turtles at sea. Thus, despite a likely increase in recruitment, the adult mortality rate calculated for the Las Baulas population by Spotila et al. (2000) indicates that it will be extirpated unless the causes of mortality are removed or controlled.

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