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Nesting Leatherback Turtles at Las Baulas National Park, Costa Rica

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Abstract. – Las Baulas National Park on the Pacific coast of Costa Rica includes three beaches, Playa Grande, Playa Langosta, and Playa Ventanas, that support a major nesting colony of leatherback turtles, *Dermochelys coriacea*. During the 1993–94 nesting season, we tagged 159 individuals with inconel tags, and 154 of these with PIT tags also. During the 1994–95 season, we tagged 462 individuals with inconel tags, and 459 of these with PIT tags also. Documented inconel flipper tag loss (10%, 1993–94; 7.4%, 1994–95) was high given the short time span of this study (November to February). In contrast, apparent loss rate of PIT tags was 3.1% in 1993–94 and 3.3% in 1994–95. Las Baulas leatherbacks were smaller than leatherbacks reported from nesting beaches outside the east Pacific area. Mean standard curved carapace length (SCCL) was 144.4 cm in 1993–94 and 147.6 cm in 1994–95. Modal internesting period was 9 days. Mean observed clutch frequency was 3.6 for the 1993–94 season and 3.5 for the 1994–95 season. Mean estimated clutch frequency was 5.1 for 1993–94 season and 4.9 for the 1994–95 season. Estimated clutch frequency was higher than observed for both seasons due to incomplete beach coverage and possibly to lack of beach philopatry. An estimated 1600 leatherbacks previously nested at Playa Grande during each of the 1988–89 and 1989–90 seasons. We estimated 202 nesting leatherbacks in 1993–94 and 469 in 1994–95. The decline in the 1993–94 season and the ensuing increase in 1994–95 in numbers of leatherbacks at Las Baulas was correlated with changes in mean sea surface temperatures in the equatorial Pacific Ocean region (El Niño). The decline in numbers of leatherbacks at Las Baulas since the high years of 1988–89 may be due to the recent increase in development in the area surrounding nesting beaches, as well as incidental catch of leatherbacks in offshore fisheries.

Key Words. – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; sea turtle; nests; clutch frequency; population size; conservation; management; Costa Rica

Leatherback turtles, *Dermochelys coriacea,* nest in tropical, and occasionally subtropical areas (i.e., Florida and South Africa). Major nesting colonies are located in Suriname, French Guiana, Mexico, and on both coasts of Costa Rica. Whereas numbers of nesting leatherbacks are increasing in some colonies (i.e., Suriname, South Africa), numbers on beaches in Mexico, Irian Jaya, and other locations are decreasing (Spotila et al., 1996). Decreases in numbers of nesting leatherbacks are often linked to anthropogenic causes (Ross, 1982).

Our ability to accurately assess the status of leatherback populations is intimately tied to our ability to accurately count the number of nesting females in a population and to determine how often those females return to the beach to lay eggs (Meylan, 1982). Because it is nearly impossible to record the complete nesting activity of every female turtle in any but the smallest populations in any given nesting season, let alone every year, it is necessary to estimate that activity. Obtaining accurate information on the number of turtles nesting in a given year, mean nesting frequency, mean internesting period, and other aspects of chelonian reproductive ecology, is central to efforts to estimate the size of a nesting population (Meylan, 1982). Therefore, if we know the values of these parameters, then, in simplest terms, the total number of nests oviposited divided by the mean number of nests per turtle per season equals the number of turtles nesting in a given season (Tucker and Frazer, 1991).

While aerial surveys can provide valuable data by giving an instantaneous count of nests over a large area (Pritchard, 1982), they fail to account for the other data that are needed for accurate estimates of nesting population size. The many limitations of these data are discussed by Meylan (1982). The only way to obtain accurate data on numbers of turtles nesting on a beach is to conduct daily ground monitoring of nests along with a tagging program so that the mean number of nests per turtle can be determined. Even so, it is possible that many leatherbacks may only nest once in a season and never return to a given beach (Hughes, 1982). This may be due to tag loss, possible mortality, and lack of nesting site fidelity. Keinath and Musick (1993) reported a

Figure 1. Las Baulas National Park, Guanacaste, Costa Rica. The shaded area indicates Park boundaries. The Park includes Playa Ventanas, Playa Grande, Playa Langosta, the Estero de Tamarindo, and the Estero San Francisco with their associated mangrove stands.

leatherback nesting on separate islands 100 km apart in the Caribbean. Another leatherback renested a distance of 80 km from Tortuguero, Costa Rica, at Bocas del Toro, Panama (Spotila, unpublished data). There is a critical need for basic studies on the population biology and reproductive ecology of leatherbacks if we are to develop effective conservation programs. These should focus on both large and small nesting colonies.

Las Baulas National Park on the Pacific coast of Costa Rica (Fig. 1) supports one of the largest leatherback nesting colonies in the Pacific (Spotila et al., 1996), and has a high population density on its three nesting beaches. The largest nesting beach, Playa Grande, recently (early 1980s) had as many as 200 leatherbacks nesting per night at the height of the season in late December and early January (Pritchard, 1990). Playa Langosta to the south had as many as 30 leatherbacks nesting per night (mean = 7–8) during December and January in 1991–92 (Chaves et al., 1996), and Playa Ventanas to the north had as many as 10 per night. Despite the importance of the Las Baulas population to the conservation of the species, and the ratification of the area as a National Park in July 1995, this area continues to be under considerable pressure from development and tourism.

In order to obtain basic information for development of a National Park management plan, we undertook a study of leatherback nesting ecology on Playa Grande during the 1993–94 and 1994–95 seasons. Our specific goals for this study were to: 1) determine numbers of leatherbacks nesting on Playa Grande, 2) determine the relationship between reproductive characteristics, such as nesting frequency and internesting interval, and estimations of population size, 3) determine the possible effect of increasing beachfront development on nest site location, and 4) compare the effectiveness of the traditional flipper tagging method to that of the newer passive integrated transponder (PIT) tag method.

MATERIALS AND METHODS

Las Baulas National Park encompasses the Bahia de Tamarindo, adjacent beaches and mangrove estuaries near Tamarindo, Guanacaste Province, in Pacific northwestern Costa Rica (10°20'N, 85°51'W). The park contains three beaches which are used by leatherbacks as nesting sites. Playa Ventanas, the northernmost of the three beaches, is 1.0 km long, Playa Grande is 3.5 km, and Playa Langosta, the southernmost beach, is 1.3 km (Fig. 1).

Chaves et al. (1996) completed a study on Playa Langosta during the 1991–92 season and Koberg collected data on the number of nests on Playa Grande and Playa Ventanas for the 1988–89 to 1992–93 seasons. Playa Grande supported the majority of leatherbacks at Las Baulas, and we therefore concentrated our efforts there.

Playa Grande is a low to medium energy crescent-shaped beach. The northern end is delineated by a rocky outcropping separating Playa Grande from Playa Ventanas. To the south the beach terminates at the Tamarindo mangrove estuary. From north to south, in 1993–95, the first 600 m of Playa Grande had a shallow slope and the highest tides washed almost to the vegetation. The next 900 m was flatter and the nightly high tide washed to a ca. 1 m high berm at the vegetation. The next 1400 m had a steeper slope and elevated plateau that was seldom washed by the tide. The last 600 m had a shallow slope and was washed by the highest tides.

We assessed leatherback nesting activity by nightly patrols from late October until late February in 1993–94 and 1994–95. Since leatherbacks at Playa Grande concentrate their nesting activity around high tide (unpublished data), our nightly patrols took place from two hours before until several hours after high tide or until sunrise. Early morning beach patrols to count nesting tracks confirmed that we encountered > 95% of nesting leatherbacks. We marked leatherbacks on the beach, during or after they laid their eggs, with both inconel flipper tags and PIT tags (glass encapsulated Passive Integrated Transponders).

We tagged leatherbacks on both hind flippers (1993–94) or on just the left hind flipper (1994–95) in the inguinal skin flap with inconel tags (National Band and Tag Co., style 681) provided by the U.S. Fish and Wildlife Service. These tags had a University of Costa Rica return address on one side and an alphanumeric code on the other. During both the 1993–94 and 1994–95 seasons, the code began with the letter V and was followed by a four digit number.

We also tagged turtles with a PIT tag in the left shoulder following the method of Dutton and McDonald (1994). PIT tags used in this study (AVID) were 14 mm x 2 mm and were injected internally into an animal with a 2 cm long, 12 gauge hypodermic needle and syringe fitted with a piston to inject the tag. We stored PIT tags in a dilute solution of 10% povidine-iodine until time of insertion. We kept the PIT tag applicator in a clean, sealed, resealable plastic bag when not in use and cleaned the applicator with an alcohol swab and the povidine-iodine solution before each use. Prior to insertion, we tested each PIT tag with the tag reader (scanner) (AVID Marketing Inc., Norco, California), to insure that the tag was functioning; we then cleaned the turtle's skin with a sterile alcohol prep pad, inserted the tag, and read the tag to verify its number. We cleaned applicator needles in povidine-iodine after each use and at the end of each night and discarded dulled needles.

At the time of oviposition or later during nest covering, we took three measurements of leatherbacks with a flexible measuring tape: 1) standard curved carapace length (SCCL), defined as the curved length from the center of the nuchal notch to the posterior carapace tip along the central ridge, 2) curved carapace length (CCL), defined as the curved maximum length from the tip of the first bony ridge to the side of the midline to the distal carapace tip, and 3) standard curved carapace width (CCW), defined as the curved distance across the carapace at the widest point of the turtle from side ridge to side ridge. We remeasured individual turtles upon subsequent encounters to assess the precision of these measurements.

We evaluated nest site selection on Playa Grande in 1994–95 using two sets of location data for each nest. First, we demarcated the length of the beach with markers every 50 m (from north to south) and recorded nests in the section corresponding to the nearest location marker to the north. For example, a nest recorded in location 18.5 indicated a nest deposited between 1850 m and 1900 m from the northern boundary of Playa Grande. Second, we divided the beach into three zones from the water to the tree line and recorded the position of nests within each section according to their zone: zone 1 was the area below the high tide line, zone 2 was between the high tide line and the vegetation, and zone 3 was in the vegetation.

We calculated internesting period for each returning female leatherback as the number of days between observed ovipositions. We did not include aborted oviposition attempts in this analysis.

We recorded observed clutch frequency (OCF) as the number of ovipositions observed during the season for an individual. However, because OCF usually underestimates the true number of clutches a female deposits during a season (Meylan, 1982; Frazer and Richardson, 1985) we also calculated an estimated clutch frequency (ECF) for each individual. Mean internesting period for leatherbacks at Las Baulas was 9 days, although we observed individuals renesting in as few as 5 days and as many as 13 days (see Results). Thus, we divided the number of days between the first and last observed oviposition by 9 and added 1 (for the first oviposition) to obtain ECF.

We used nest count data from the 1988–89 season to the 1994–95 season to determine population trends at Playa Grande. Data from prior seasons when we were not present were collected by Dona Esperanza Rodriguez Rodriguez of Playa Grande during daily sunrise beach surveys. She also collected independent nest count data during the time that we were collecting our own data. Comparison of her daily counts to those of our research team during those nesting seasons and months for which we were present agreed within 5% per night. Thus, we were confident in her data for the prior years.

For all years we calculated population estimates as follows. We first determined the mean number of nests per night for the months of November through February, since in some cases data were incomplete or nest counts were missing for some nights. Then we multiplied the mean nightly number of nests for each month by the number of nights in that month, to obtain number of nests per month. We added these figures for all months, resulting in a total number of nests per season. Then we divided the total number of nests by the mean ECF (= 5) obtained from our data to estimate a nesting female population for each season. We used a value of 5 since ECF for the 1993–94 and 1994–95 seasons were 5.1 and 4.9, respectively (see Results).

We analyzed data following Sokal and Rohlf (1981) using descriptive statistics, ANOVA, t-test, G-test of independence, and regression analysis.

RESULTS

Nests. — During the 1993–94 season, we recorded a total of 625 leatherback nests at Las Baulas, of which 605 were on Playa Grande, and during the 1994–95 season, we recorded a total of 1638 leatherback nests at Las Baulas, of which 1548 were on Playa Grande. Since we made only

Table 1. Measurements of nesting leatherbacks (*Dermochelys coriacea*) at Las Baulas National Park during the 1993–94 and 1994–95 nesting seasons. All three measurements demonstrate a significant difference ($P \leq 0.05$) between seasons. SCCL = standard curved carapace length; CCL = maximum curved carapace length; CCW = curved carapace width.

Measurement	Season	Mean (cm)	SD (cm)	Min (cm)	Max (cm)	n	F-value	df year, error	P
SCCL	1993–94	144.37	6.92	124.6	164.0	156			
	1994–95	147.57	6.40	125.0	171.0	441	27.519	1, 595	.0001
CCL	1993–94	150.08	7.10	128.3	167.0	156			
	1994–95	152.78	6.76	132.0	185.0	441	17.896	1, 595	.0001
CCW	1993–94	103.89	5.31	90.3	122.3	156			
	1994–95	105.26	4.77	82.0	123.0	441	8.893	1, 595	.0030

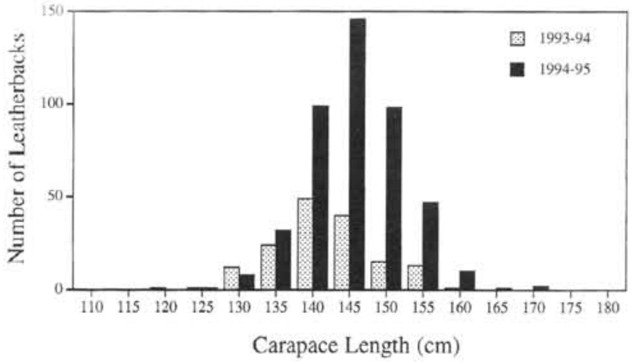

Figure 2. Size frequency distribution (SCCL) for leatherbacks (*Dermochelys coriacea*) nesting on Playa Grande during the 1993–94 and 1994–95 seasons.

occasional surveys on Playa Ventanas and Playa Langosta during the course of other studies, numbers of nests recorded at these two beaches were not used in our analysis of population size.

Tagging. — During the 1993–94 season, we tagged 159 individuals with double inconel tags, and 154 of these with PIT tags also. During the 1994–95 season, we tagged 462 individuals with inconel tags, and 459 of these with PIT tags also. During the 1993–94 season we observed 130 individuals (82%) nesting at least twice. Of those, 13 (10%) had lost at least one inconel tag. During the 1994–95 season we observed 363 individuals (79%) nesting at least twice. Of those, 27 (7.4%) had lost their inconel tag. During the 1993–94 season, 4 (3.1%) of 130 returning leatherbacks received two PIT tags. Three were due to the failure of the initial PIT tag, while one was due to experimental error. During the 1994–95 season, 12 (3.3%) of 363 returning leatherbacks received two PIT tags. Four were due to failure of the initial PIT tag and eight were due to experimental error. Normally scanners registered a PIT tag immediately. However, occasionally it took several scans (up to 40) to register a PIT tag. Experimental error included: 1) occasions when the scanner did not register the initial PIT tag, though it registered the PIT tag on subsequent occasions, 2) scanner malfunction, or 3) failure of the researcher to check for the presence of or to register a previously implanted PIT tag.

We observed only one remigrant leatherback that was flipper-tagged in an earlier year despite the extensive tagging efforts at Las Baulas in past years. Chaves et al. (1996) tagged 215 leatherbacks on Playa Grande in 1991–92 and 62 leatherbacks on Playa Langosta from 1987 to 1991 and observed two remigrants in 1991–92. In addition, they tagged 229 leatherbacks on Playa Langosta in 1991–92, but we did not observe any of these turtles during our visits to that beach. We did observe apparent "tag scars" on some turtles on both beaches, but in most cases it was difficult to distinguish between "tag scars" and scars from other causes. In December, 1993 we observed a turtle to which we had attached a satellite transmitter in January, 1991. We reidentified the turtle by scars left in its caudal carapace tip from the attachment of the satellite transmitter. At that time we also observed another turtle which had been used in a physiology experiment in January, 1992. We reidentified that turtle by an obvious scar in its caudal carapace tip as well. In both cases the turtles had been double tagged with flipper tags in the inguinal area. However, in both cases no tags were retained, the skin was completely healed, and there was no indication that they had ever been tagged. These data indicate that flipper tags may have been lost from many of the turtles at Las Baulas tagged in previous years.

Nesting Beach Fidelity. — From December, 1994 to February, 1995 biologists from Programa Rescate Tortugas Marinas, Costa Rica, recorded a total of 1196 leatherback nests on Playa Langosta (S. Rodriguez, *pers. comm.*). Since these researchers did not conduct a simultaneous tagging program we could not fully assess the degree of nesting fidelity for each beach. However, we observed 1 of 14 leatherbacks that we tagged on Playa Langosta later nesting twice on Playa Grande. We tagged 28 leatherbacks on Playa Ventanas, and observed 5 nesting there again and 5 nesting on Playa Grande at least once. Of 420 leatherbacks tagged on Playa Grande, we observed 23 nesting on Playa Ventanas and 15 on Playa Langosta. This preliminary effort on Playa Langosta and Playa Ventanas indicated that there was some nesting exchange among the three beaches.

Size. — Leatherbacks nesting at Playa Grande during the 1993–94 season were smaller than those nesting during the 1994–95 season (144.4 ± 6.9 cm vs. 147.6 ± 6.4 cm SCCL; 150.1 ± 7.1 cm vs. 152.8 ± 6.8 cm CCL; 103.9 ± 5.3 cm vs. 105.3 ± 4.8 cm CCW; Table 1). There was a statistically significant trend (t-test, $P < .0001$) for increased size in the 1994–95 leatherbacks as determined for SCCL (Fig. 2).

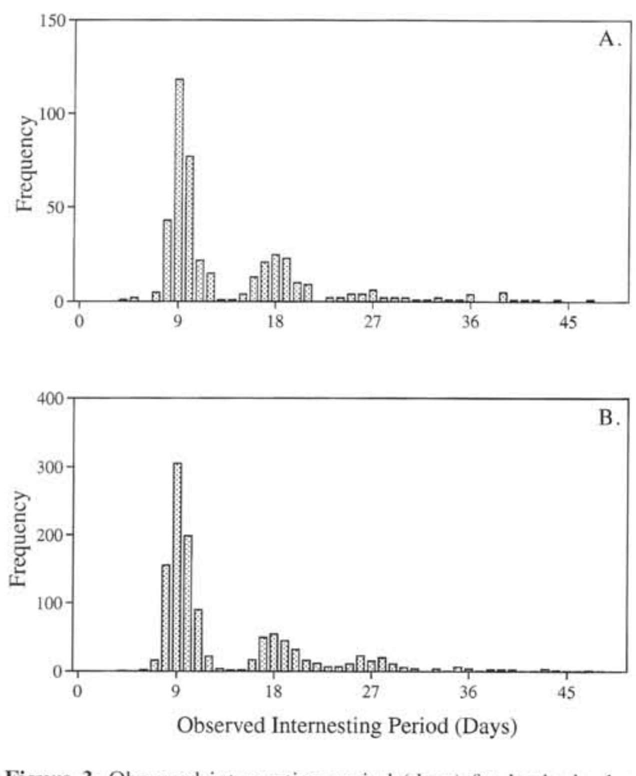

Figure 3. Observed internesting period (days) for leatherbacks nesting on Playa Grande during the (A) 1993–94 and (B) 1994–95 seasons.

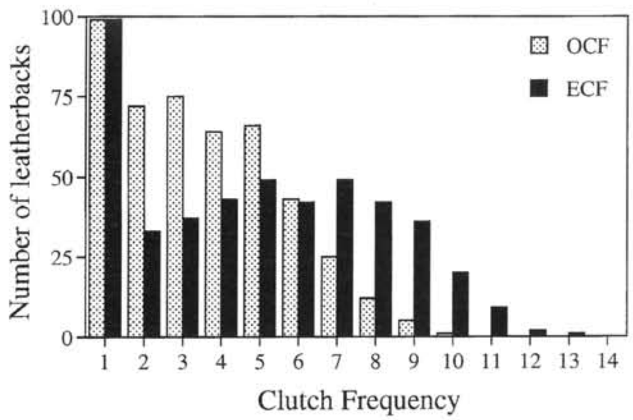

Figure 4. Distribution of observed clutch frequency (OCF) and estimated clutch frequency (ECF) for leatherbacks nesting on Playa Grande during the 1994–95 season.

Internesting Period. — Internesting periods were similar in both seasons (Fig. 3). Internesting period mode for both seasons was 9 days with a mean internesting period of 9.4 days ($n = 438$) for the 1993–94 season and 9.3 days ($n = 1175$) for the 1994–95 season. We excluded intervals > 14 days from this analysis because we assumed that we either missed the turtle's oviposition on Playa Grande, or that it nested on another beach. Data from both seasons exhibited peaks at 8–11 days, 16–20 days, and small peaks at 25–28 days. These later internesting periods greater than 8–11 days were presumably the result of turtles we had missed on their previous return(s) or which had nested elsewhere.

Nesting Frequency. — Observed clutch frequency (OCF) ranged from 1 to 10 clutches in both seasons (Fig. 4). Mean OCF was 3.6 ($n = 159$, SD = 2.14) in the 1993–94 season and 3.5 ($n = 462$, SD = 2.07) for the 1994–95 season. During the 1994–95 season, the majority of individuals (53.3%) that we observed nested three times or less. Estimated clutch frequency (ECF) (Fig. 4) ranged from 1 to 12 in the 1993–94 season and 1 to 13 in the 1994–95 season. Mean ECF was 5.1 ($n = 159$, SD = 3.17) in the 1993–94 season and 4.9 ($n = 462$, SD = 3.03) in the 1994–95 season. During the 1994–95 season, even when we used ECF as a measure of clutch frequency, the majority of leatherbacks (56.5%) were estimated to have nested five times or less. Although this figure represents a more realistic assessment of leatherback nesting frequency, it may still be an underestimate of leatherback nesting frequency.

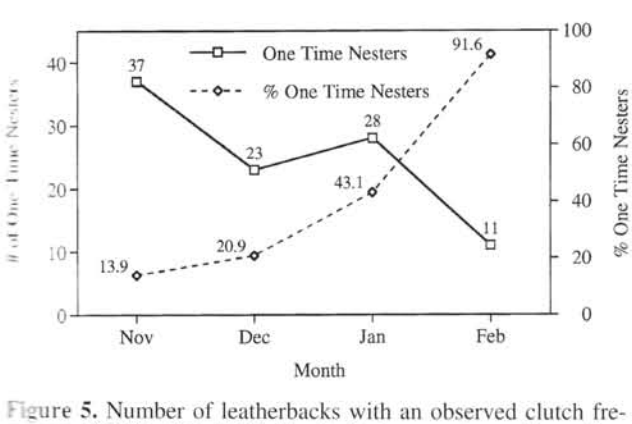

Figure 5. Number of leatherbacks with an observed clutch frequency (OCF) of 1. Solid line indicates numbers of one-time nesters for each month. Dotted line indicates the percentage of one-time nesters as a function of newly tagged turtles for that month. Thus, though there were 37 observed one-time nesters in November, they accounted for a relatively small percentage of the total individuals tagged that month. In contrast, though we recorded 11 one-time nesters in February, they accounted for a large percentage of leatherbacks tagged that month.

Ninety-nine individuals were seen to nest at Playa Grande only once (Fig. 4) during the 1994–95 season (21.4%). Although we observed greater numbers of one-time nesters early in the season, the relative proportion of one-time nesters to total number of leatherbacks tagged in the same month increased throughout the season (Fig. 5). There was no significant difference in the mean SCCL of one time nesters (146.6 cm) and the 1994–95 population as a whole (147.6 cm; $P = 0.1968$).

Nest Location and Zone. — Distributions (north-south placement) of leatherback nests along Playa Grande for both the seasons (Fig. 6) were non-random (G-Test, 1993–94: $G = 669.2$, df = 25; 1994–95: $G = 1516.9$, df = 25). During both seasons nests tended to be more centrally located, away from the extreme northern and southern sections of the beach. Nests laid during the 1994–95 season were more centrally located than those laid during the 1993–94 season (G-Test, $G = 60.0$, df = 8). Sections 21 and 22 and sections 24 and 26 experienced the greatest nesting activity in the 1994–95 and

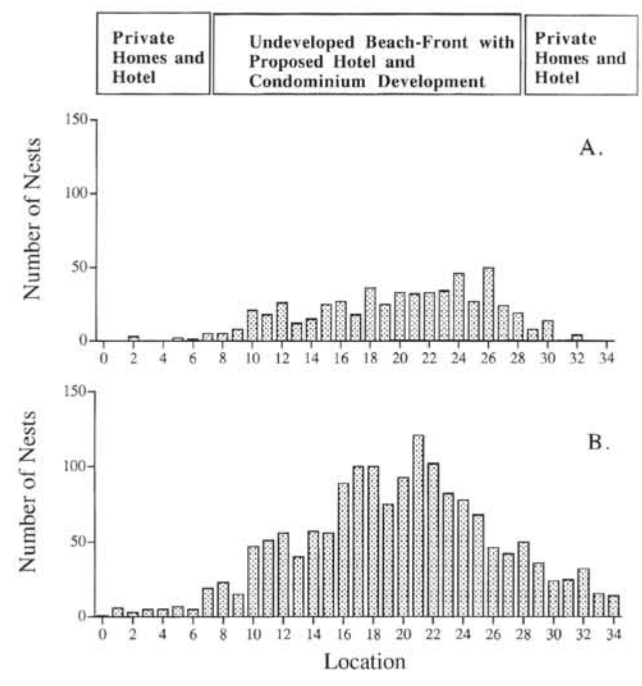

Figure 6. Distribution of leatherback nests on Playa Grande during the (A) 1993–94 and (B) 1994–95 seasons. Location numbers refer to 100 m sections from north to south. Above the distribution graphs are the locations of existing and proposed beach front development on Playa Grande. Beach front development is defined as construction which is less than 100 m from the mean high tide line. The area of private homes and hotel near the southern end of the beach was expanded between the 1993–94 and 1994–95 seasons, contributing to more lighting. The 1994–95 distribution of nests is shifted slightly to the north as compared to the 1993–94 season.

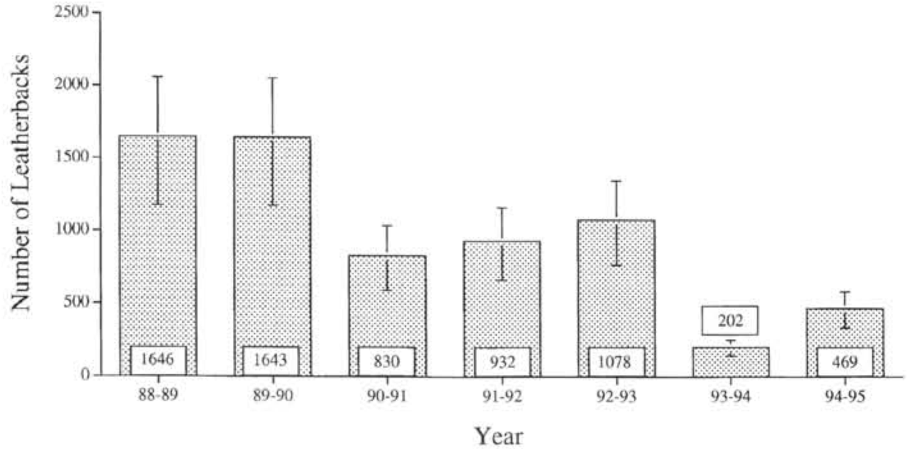

Figure 7. Estimates of numbers of nesting leatherbacks at Playa Grande from the 1988–89 season through the 1994–95 season based on an estimated clutch frequency (ECF) of 5. The top error bar reflects an ECF of 4, the bottom error bar an ECF of 7.

1993–94 seasons, respectively. During both seasons nesting was minimal in the north end (sections 0–9).

We recorded beach zone location for 1387 nests in the 1994–95 season, of which 119 (8.6%) were laid in zone 1 (below the high tide line), 1193 (86.0%) in zone 2 (between high tide line and vegetation), and 75 (5.4%) in zone 3 (within vegetation). Nest distribution in the three zones was not random (G-Test, $G = 861$, $df = 2$) and there were also within-season differences. As the season progressed, the proportion of nests in zone 2 increased, while the proportion in zones 1 and 3 decreased (G-Test, $G = 58.7$, $df = 6$).

Nesting Population Size. — Estimated numbers of leatherbacks nesting at Playa Grande (total nests/mean ECF) decreased from the 1988–89 season through the 1994–95 season (Fig. 7). During the 1988–89 and 1989–90 seasons, Playa Grande received an estimated 1646 and 1643 individual nesting leatherbacks, respectively. The number of leatherbacks declined dramatically to 830 in 1990–91 and to a low of 202 individuals during the 1993–94 season, an 88% decline from the 1988–89 season. In 1994–95 numbers increased to 469. In addition, using the number of nests reported for Playa Langosta in 1994–95 (S. Rodriguez, *pers. comm.*) we calculated that 239 leatherbacks nested there. Thus, Playa Langosta supported 51% as many turtles as Playa Grande.

The overall temporal nesting distribution was similar among years from the 1988–89 season to the 1994–95 season, though numbers of leatherbacks nesting nightly was considerably different between seasons. While there was some scattered nesting from March to September with a mean of < 1 to 1 turtle per night from May to August, and 1–3 per night in April and September, nesting typically in-

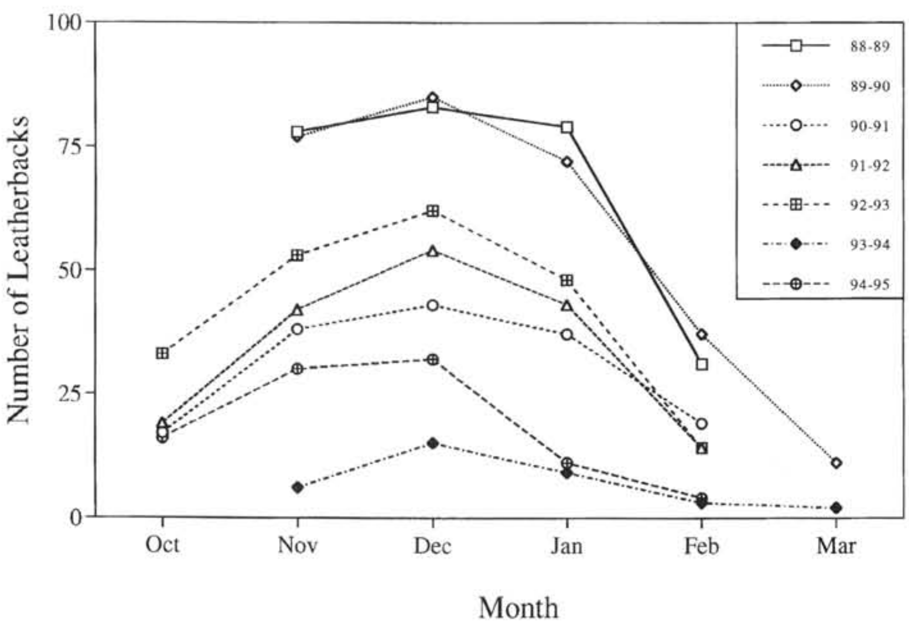

Figure 8. Mean nightly number of leatherbacks per month nesting on Playa Grande from the 1988–89 season through the 1994–95 season.

creased dramatically in October. Nesting then approximately doubled in November, peaked in December, remained high in January, declined rapidly in February, and tapered off in March (Fig. 8). During the 1988–89 and 1989–90 seasons, mean number of leatherbacks nesting per night in December was > 80, while during the 1993–94 and 1994–95 seasons these numbers were 15 and 32, respectively.

DISCUSSION

Las Baulas National Park consists of three beaches, Playa Grande, Playa Langosta, and Playa Ventanas, that host a major nesting colony of leatherbacks. Another important nesting beach for leatherbacks on the Pacific coast of Costa Rica is Playa Naranjo in Santa Rosa National Park, located 57 km to the north of Las Baulas. Numbers of tracks recorded there during the 1983–84 and 1989–90 seasons were 312 (Cornelius and Robinson, 1985) and 466 (Arauz-Almengor and Morera-Avila, 1994), respectively. Using our ECF of 5 we estimate that these correspond to 62 and 93 nesting leatherbacks. In 1990–91 Arauz-Almengor and Morera-Avila (1994) recorded 1212 nests at Playa Naranjo, which would indicate an estimated 242 leatherbacks nested on the beach during that period. Anecdotal reports indicate that small numbers of leatherbacks also nest on other beaches to the north and south of Las Baulas, such as Playa Cabuyal, Playa Nancite, and the Osa Peninsula. Additional research is needed to determine the extent of nesting on beaches outside Las Baulas Park.

The concentrated leatherback nesting on a few Pacific beaches in Costa Rica may be due to two factors. First, sandy beaches on the Pacific coast are discontinuous and often separated by rocky areas which are unsuitable for leatherback nesting. Second, there has been significant development on several beaches, such as Playa Tamarindo and Playa Flamingo, which once hosted leatherback nesting. In contrast to this pattern, there is widespread nesting of leatherbacks on the Caribbean coast of Costa Rica from Nicaragua to Panama. Hirth and Ogren (1987) stated that leatherback nesting density is similar over the area from Río Tortuguero to Puerto Limon and Leslie et al. (1996) estimate that 150 to 368 leatherbacks nest there. Further south at the Gandoca-Manzanillo National Wildlife Refuge near the Panamanian border, Chacón (1996) tagged 309 leatherbacks in 1995. The reason for this pattern is that there are large areas of contiguous beach on the Caribbean coast, with only a few areas, like Punta Cahuita and the Puerto Limon area, that are too rocky for nesting. Also, development is limited in most areas. Thus, leatherbacks on the Pacific coast of Costa Rica are concentrated in smaller areas that are more vulnerable to disruption.

Tagging. — Tag return data is central to our understanding of the demography and reproductive ecology of leatherbacks. Within season inconel flipper tag loss (10% in 1993–94; 7.4% in 1994–95) was notable given the short time span of this study. Combined inconel tag loss for both seasons was 8.1%. In all cases of tag loss, tags appeared to rip out. In addition, we expect that tag loss would be higher during migration, feeding, and diving activities during the years between nesting events. Thus, most individuals with a nesting cycle greater than two years probably lose their tags, leading to overestimates of nesting population size and global population size. While some flipper tags (especially titanium) have remained on some leatherbacks for up to 5 years (Hughes, 1982, 1996) our data suggest that inconel flipper tag loss in leatherbacks is high, and that inconel flipper tagging is not a reliable method for long term leatherback studies.

We found PIT tags to be more reliable than flipper tags. The PIT tag loss was not necessarily a loss of tag per se, but an inability to read a previously implanted tag. Apparent loss rate was 3.1% in 1993–94 and 3.3% in 1994–95. In some cases, PIT tag failure occurred immediately: a total of 7 PIT tags (1.4%) could not be read subsequent to initial application. In these cases, cause of failure was unknown, though it may have been due to movement of the tag within the body beyond the range of the scanner, or malfunction of the PIT tag itself. In the remaining 9 cases (1.8%), we attributed PIT tag failure to experimental error. Our data indicate that PIT tags were more reliable than inconel flipper tags: PIT tag loss rate was lower than inconel tag loss rate during both years of this study. However, we recommend the use of both PIT tags and flipper tags whenever possible, because flipper tags are easily recognized and read during studies on nesting beaches and PIT tags allow more accurate assessments of local, regional, and global female leatherback population sizes.

Size. — Las Baulas leatherbacks are similar in size to other East Pacific leatherbacks but smaller than leatherbacks elsewhere. Mean SCCL was 144.4 cm on Playa Grande in 1993–94, 147.6 cm in 1994–95, 150 cm in 1990 (Guadamuz Rosales, 1990), and 147 cm on Playa Langosta in 1991–92 (Chaves et al., 1996). Leatherbacks on Playa Naranjo had a mean SCCL of 141 cm in 1971–72 (Cornelius, 1976) and those at Tierra Colorada, Mexico had a mean SCCL of 146.1 cm in 1977 (Pritchard, 1982). West Pacific leatherbacks nesting in Irian Jaya had a SCCL of 161 cm (Starbird and Suarez, 1994), and Indian Ocean leatherbacks nesting in Tongaland, South Africa had a mean SCCL of 162.2 cm in 1964–68 and 159.6 cm in 1994–95 (Hughes, 1996). Caribbean leatherbacks are also larger. Mean SCCL of leatherbacks from the Caribbean coast of Costa Rica was 156. 2 cm (Leslie et al., 1996) and 152.8 cm (Hirth and Ogren, 1987). Leatherbacks at St. Croix had a mean SCCL of 152.9 cm (Dutton et al., 1994) and Tucker and Frazer (1991), using a regression equation relating straight-line carapace length to SCCL, reported a mean SCCL of 154 cm for leatherbacks at Culebra, Puerto Rico. Mean straight line carapace length of leatherbacks in French Guiana in 1988 was 154.0 cm (Fretey and Girondot, 1989). Using the linear regression relating straight-line carapace length to over the curve carapace length provided by Tucker and Frazer (1991), we computed a mean SCCL of 162 cm for French Guiana. The significance of the small size of East Pacific leatherbacks is unclear. It may be that these leatherbacks are younger turtles than those nesting at other beaches. It is also possible that these turtles may be the same age, but have slower growth rates and mature at smaller sizes than leatherbacks in other populations. Hughes (1996) attributed the decline in leatherback size at Tongaland from 1964–68 to 1994–95 to the presence of many more younger, and smaller females. Leatherbacks at Las Baulas were as small as 120 cm with many turtles less than 140 cm. Protection of Las Baulas beaches from egg poachers began in 1988. Given the estimates of rapid growth rates and a possible 6 to 13 year time to sexual maturity for leatherbacks (Rhodin, 1985; Zug and Parham, 1996), it is intriguing to speculate that the small leatherbacks nesting at Las Baulas are turtles which were recruited to the population after protection was provided to these beaches.

Nesting Frequency. — Internesting period at Las Baulas was 9 days which is similar to values reported at other leatherback beaches (Eckert, 1987; Fretey and Girondot, 1988; Tucker and Frazer, 1991; Starbird and Suarez, 1994).

Mean observed clutch frequency (OCF) at Playa Grande for the 1993–94 season (3.6) and the 1994–95 season (3.5) was lower than mean OCFs reported for small nesting populations and larger than those for very large populations. Observed clutch frequencies for leatherbacks at Sandy Point, St. Croix, were almost double those at Las Baulas. Eckert (1987) reported mean OCFs of 4.9 to 7.0 for 1982–87, and Dutton et al. (1994) reported a mean OCF of 5.9. These values are similar to those for leatherbacks nesting at Culebra, Puerto Rico (OCF of 5.2 to 7.0) (Tucker and Frazer, 1991). Fretey and Girondot (1989) counted a mean OCF of 2.81 for leatherbacks nesting in 1988 in French Guiana, where 5502 leatherbacks were tagged that season. High OCFs reported for small populations on small beaches and low OCFs reported for large populations and large beaches are probably a function of sampling effort expended per female; that is, the effectiveness of beach coverage in time and space. Small nesting populations also had a high percentage of total nesting occurring within study site boundaries (> 90%) (Tucker, 1989). Fecundity may be underestimated for large populations and large beaches which cannot be patrolled intensively (Tucker, 1989). We expect that complete coverage of all three beaches at Las Baulas would result in an OCF that is closer to those reported for smaller populations.

At Las Baulas, mean estimated clutch frequency (ECF) was 5.1 and 4.9 for 1993–94 and 1994–95, respectively. This was similar to the ECF of 4.6 reported by Fretey and Girondot (1989) for leatherbacks in the large French Guiana colony, but was lower than the ECFs of 5.8 to 7.5 reported by Tucker and Frazer (1991) for leatherbacks nesting at the small Culebra colony from 1984–87. Differences between reported OCF and ECF for Culebra were not great, indicating that beach coverage was intensive and few nestings were missed during the study period. In comparison, the difference between OCF and ECF reported by Fretey and Girondot (1989) was much greater, indicating that many nestings were missed. The difference between OCF and ECF in our study falls between that of Tucker and Frazer (1991) and Fretey and Girondot (1989), also indicating that more complete beach coverage at Las Baulas is necessary to better determine the true clutch frequency. However, mean ECF provides an adequate estimate of true clutch frequency, especially in areas where complete beach coverage is difficult due to large population size or large nesting beach size.

Table 2. Distribution of estimated clutch frequency (ECF) of Playa Grande leatherbacks by month in which they were first tagged. Month had a statistically significant interaction on ECF ($F = 27.382$, $P = 0.0001$).

	Mean	SD	n
November	5.76	2.99	266
December	4.98	2.81	119
January	2.58	1.77	57
February	1.11	0.35	10

Fretey and Girondot (1989) demonstrated that both OCF and ECF declined as a function of the time of season that individual leatherbacks were first tagged. The OCF and ECF were higher when considering those leatherbacks that were tagged in the beginning of the nesting season (April). Conversely, OCF and ECF were lower when considering those turtles that were tagged later in the season (August). The authors suggested that this was due to tagging of turtles late in the season subsequent to several prior unobserved ovipositions. We suggest an alternative interpretation for our data. Late season one-time nesters contributed to the low OCF and ECF because our efforts on Playa Grande concluded shortly after these leatherbacks began their nesting season. An analysis of ECF as a function of tagging date shows ECF did decrease as a function of tagging date (Table 2). Individuals tagged earlier in the season (i.e., November) had a higher ECF than did individuals tagged late in the season (i.e., February). While numbers of one-time nesters in the 1994–95 season decreased as the season progressed, they accounted for a greater proportion of individuals tagged in January and February than earlier (Fig. 4). Proportions of one-time nesters at Playa Grande increased during the later part of the nesting season because frequency and coverage of nightly patrols decreased in February and then ended, and we missed subsequent nesting episodes in March. It is also possible that leatherbacks first tagged in January or February had been nesting elsewhere previously or were just beginning to nest but were on their way to another nesting beach. Understanding the reproductive pattern of these one-time nesters is important in obtaining accurate OCF and ECF estimates. Hughes (1982) stated that many leatherbacks at Tongaland in South Africa nest only once and do not return. Clearly, one-time nesters are still a mystery within and between seasons on many beaches, and will continue to confound estimates of OCF and ECF until beach coverage on large beaches and for large populations becomes more complete.

Location and Zone. — The placement of nests along Playa Grande during both the 1993–94 and 1994–95 seasons was non-random (Fig. 6), with a negative correlation between nest distribution and beachfront development. Little nesting activity took place at the northern and southern extremes of Playa Grande where development existed. In both seasons, nesting occurred in the undeveloped central area of the beach. This suggests that development and/or lights may affect leatherback nest selection on Playa Grande. A similar nesting distribution was reported in 1990 (Guadamuz Rosales, 1990), when beachfront development was already present. Chaves et al. (1996) reported that leatherbacks on Playa Langosta also tend to nest in the central portion of the beach. Although there is no development on Playa Langosta, northern sections of the beach contain a very high berm and are immediately backed by an estuary, and the southern end of the beach is fronted by rocky outcrops so that both ends are unsuitable for leatherback nesting.

Leatherbacks nested in the open sand section of Playa Grande. The majority of nests on Playa Grande were laid in zone 2, the open sand area between the high tide line and vegetation, while few nests where laid below the high tide line (zone 1) or in the vegetation (zone 3). A lower proportion of nests were washed over by sea swell than reported elsewhere (Whitmore and Dutton, 1985; Leslie et al., 1996). Conservation efforts elsewhere have included relocating nests in danger of being washed over by sea swell, as frequent inundation reduces hatching success (Whitmore and Dutton, 1985). This is not the case at Playa Grande, where relatively few nests are inundated.

Nesting Population Size. — An estimated 1600 leatherbacks nested at Playa Grande during each of the 1988–89 and 1989–90 seasons. The number of turtles then declined to 202 in 1993–94. During the 1994–95 season, the population increased to 469. This decline was in contrast to increases in numbers of leatherbacks in some areas, i.e., South Africa (Hughes, 1996), French Guiana (Fretey and Girondot, 1989), and St. Croix (Boulon et al., 1996). We based nesting population estimates in this study on nest counts, assuming a mean ECF of 5 clutches per individual. However, population estimates vary considerably depending upon the clutch frequency used in the population estimates (Tucker and Frazer, 1991). Therefore, we also provide error estimates for our population sizes (Fig. 7). For example, a decrease of ECF to 4, a number near ECFs for large populations (Fretey and Girondot, 1989), would increase our estimated population size for 1994–95 from 469 to 586. An increase of ECF to 7, a number like that of ECFs for small populations with relatively complete coverage (Eckert, 1987; Tucker and Frazer, 1991) would decrease our estimated population for 1994–95 to 335. This large error margin indicates the importance of correctly determining clutch frequency for a population, because any error in that estimate translates into a large error in the population size estimate.

Intensity of beach coverage, duration of coverage (i.e., for a few days, weeks, or the entire season), and type of coverage (i.e., counting nests, counting turtles, or tagging turtles) influence the accuracy of nesting population size estimates. If a baseline clutch frequency has been determined for the nesting population, nests counts may be acceptable. However, it is important to note that differences in reproductive output due to temporal and spatial variability in accumulated energy may be realized as changes in fecundity, which may in turn lead to either a change in numbers of eggs per clutch or in numbers of clutches per season. Thus, assuming equal clutch frequencies between seasons may lead to inaccurate nesting population estimates.

Pritchard (1982) advocated using aerial surveys and short term nest counts over a few days to estimate numbers of leatherbacks nesting on a beach. While this is a useful first estimate of the size of a nesting population, counting or estimating the total nestings over 9–10 mid-season nights may also lead to large errors in population estimates. This method makes two important assumptions. The first is that numbers of nesters per night for one week to the next are evenly distributed. That is, there is little variation in numbers of nesters from one night to the next, or one week to the next. This is not the case on Playa Grande. Numbers of nesting leatherbacks vary from one week to the next. The second assumption is that numbers of nesters will increase and decrease in a predictable pattern from one year to the next. The temporal pattern of numbers of nesters in different nesting seasons is not the same (Fig. 8). Thus, picking a 10 day period in mid-season (early December at Playa Grande) to estimate population size could result in considerable error. For example, we calculated a nesting population size of 314 individuals for the 1994–95 season when we extrapolated nest counts from a randomly chosen 10 day period in December to the whole season, in comparison to an estimate of 469 leatherbacks when using data for the entire season. This approach would also induce errors when comparing population estimates in 1994–95 to 1990–91, 1991–92 and 1992–93. Therefore, care must be taken in extrapolating from one 10 day period to an entire season.

There are several factors which may explain the decline in numbers of leatherbacks nesting at Playa Grande from 1988–89 to 1994–95. One possible cause for this decline may be the occurrence of an El Niño Southern Oscillation (ENSO) in the Pacific during the early 1990s. Limpus and Nicholls (1990) reported that numbers of nesting green turtles in Australia varied from year to year during the 1980s while the number of female turtles at feeding grounds remained constant. They found a correlation between mean atmospheric pressure measurements at Darwin, Australia (an index of ENSO) and numbers of nesting turtles. The decline in numbers of nesting green turtles lagged two years behind the correlated pressure measurement, which the authors attributed to the time needed for turtles to prepare for a breeding season. We saw a similar pattern when we compared equatorial Pacific sea-surface temperatures (SST, an index of ENSO, averaged over the Pacific Ocean NIÑO3 region, 5°S to 5°N, 90°W to 150°W; Chen et al., 1995) with numbers of nesting leatherbacks at Playa Grande. The decrease in numbers of leatherbacks nesting at Playa Grande since the 1989–90 season corresponds with an increase in SST (data from Chen et al., 1995). A recent peak increase in SST occurred during the 1991–92 season, which corresponded with the lowest estimated leatherback nesting population which we recorded at Playa Grande in the 1993–94 season, allowing for a two year time lag as observed by Limpus and Nicholls (1990). The increase in numbers of leatherbacks in 1994–95 corresponded with a drop in SST two years earlier in 1992–93. Changes in surface currents and upwellings may affect SST, which may in turn affect resource availability to leatherbacks that are preparing for a breeding season. Changes in resource availability may affect reproductive output and growth (Bjorndal, 1985). There was a small increase in SST in 1992–93 followed by a decline and stability in SST in 1993–94. If this correlation holds we would expect a similar or increased number of leatherbacks nesting at Las Baulas during the 1995–96 and 1996–97 seasons.

While El Niño events may be responsible for short term fluctuations in Playa Grande leatherback nesting numbers, they do not account for the long term continued decreases from the 1988–89 season to the 1994–95 season. Intense poaching of eggs (> 90% of all nests) up until the 1990–91 season at Las Baulas presumably contributed to the decline by diminished recruitment to the population. Since that time, the combination of increased conservation actions by public officials and private citizens of Costa Rica, the presence of armed guards, and increased presence of researchers on Playa Grande, have decreased poaching of leatherback nests to almost zero (Schwandt, 1994). This may explain the increased number of small (perhaps young) leatherbacks nesting on Playa Grande in 1994–95. While drift net and long line fishing have been implicated in the deaths of leatherbacks in the Pacific (Wetherall et al., 1993), we do not know the extent to which these activities were responsible for the dramatic decline of leatherbacks at Las Baulas. If the cause of the decline was egg poaching before 1990, and the time to maturation of this species is as short as 6 to 13 years (Rhodin, 1985; Zug and Parham, 1996), then we expect that the population at Las Baulas will continue to increase in the next few years. If the primary cause of the decline was incidental capture at sea, then we expect the long term trend to be a continued decline.

It is difficult to assess the impact of beachfront development on numbers of nesting leatherbacks on Playa Grande. However, the increase in development and tourism is correlated with a decrease in numbers of nesting leatherbacks. In recent years development of Playa Grande has included construction of houses and hotels at the northern and southern ends of the beach. Although effects of lights on leatherbacks are not completely known, lights are known to have a negative effect on other nesting sea turtles (Witherington, 1992). The proportionate number of leatherbacks nesting at Playa Langosta has increased since development at Playa Grande has increased. While complete coverage of Playa Grande and Playa Langosta will be necessary to determine the extent of nest site fidelity between the two beaches, increased development and lighting on Playa Grande may be encouraging leatherbacks to nest on Playa Langosta.

Conservation Implications. — The leatherback nesting colony at Las Baulas is the largest in the Pacific (Spotila et al., 1996). Conservation of leatherbacks and their nesting habitat there is central to conservation of this species in the eastern Pacific. In addition to habitat protection, continued research is needed to more completely understand the reproductive ecology of leatherbacks at Las Baulas. While it is apparent that some individuals lay up to 13 clutches in a season, complete coverage on the three nesting beaches throughout the season is required to obtain accurate measures of clutch frequency. This is essential to accurate population estimates. The combined use of PIT tags and flipper tags is useful in several ways, including long-term marking, recognition of individuals whenever or wherever encountered, and calibration of population estimates based on flipper tag returns. Improved regulations governing lighting and beach front development on Playa Grande, and their enforcement, combined with complete protection on Playa Langosta, are necessary to insure the long-term survival of leatherbacks in the eastern Pacific.

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