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Estimation of the Net Nesting Effort of Olive Ridley Arribada Sea Turtles Based on Nest Densities at Ostional Beach, Costa Rica

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Abstract.—Ostional Beach, Costa Rica, supports a large mass nesting (arribada) aggregation of Olive Ridley Sea Turtles (*Lepidochelys olivacea*). A large number of egg clutches is lost to egg harvest and to nest destruction by nesting females after every arribada. Accordingly, the purpose of our study was to generate estimates of the net number of clutches left incubating from clutch densities with the use of a quadrat methodology, and to compare these data with nesting population estimates resulting from the strip transect in time methodology that is currently applied. After the conclusion of each arribada, we randomly performed 50 excavations in 1-m^2 quadrats to count the number of clutches present. We extrapolated quadrat density data to the entire nesting area of the beach to estimate the total number of clutches remaining following each arribada and egg harvest. The mean total clutch density was 4.09 $\pm$ 0.18 SE nests/m^2. Our results showed that quadrat and transect estimate differences ranged from 0.04 to 52.6%, with quadrat estimates typically being lower. Our results demonstrated that, in the rainy season, a large number of clutches (47.4–99.9%) was left incubating in the beach after every arribada and egg harvest. By omitting clutches that were harvested or destroyed throughout the arribada, we evaluated the reproductive potential and estimated the magnitude of clutch loss on Ostional Beach, both of which play important roles in the management of the egg harvest as a sustainable conservation strategy.

Resumen.—Playa Ostional, Costa Rica presenta el anidamiento masivo o arribada de la tortuga marina Lora (*Lepidochelys olivacea*). Un número elevado de huevos se pierde durante cada arribada debido a la cosecha de huevos y a la destrucción de nidos por parte de tortugas anidadoras. Así pues, el objetivo de este estudio fue el de generar estimados del número neto de nidos que permanecen incubándose a partir de la densidad de nidos utilizando una metodología de cuadrantes y la comparación de estos datos con los estimados poblacionales obtenidos con la metodología de transectos fijos sobre el tiempo que se está utilizando actualmente. Después de la conclusión de cada arribada, realizamos al azar 50 excavaciones en cuadrantes de 1m^2 para contar el número de nidos presentes. Nosotros extrapolamos los datos de densidad de estos cuadrantes a la playa de anidación entera para estimar el número de nidos que quedan en la playa luego de cada arribada y de cada cosecha de huevos. La densidad promedio total de nidos fue de 4.09 $\pm$ 0.18 SE nidos por m^2. Nuestros resultados mostraron que las diferencias entre los estimados transectos y de cuadrantes variaron de entre 0.04% a 52.6%, siendo los estimados de cuadrantes típicamente menores. Nuestros resultados demostraron que en la época lluviosa un gran número de nidos (entre el 47,4% y el 99,9%) permanecieron incubándose en la playa luego de cada arribada y cosecha de huevos. Al omitir los nidos que son destruidos por las tortugas durante cada arribada o cosechados, este nuevo procedimiento nos permitió hacer una evaluación del potencial reproductivo y de la magnitud de la destrucción de nidos en playa Ostional, ambos siendo factores que juegan un papel importante en el manejo de la cosecha de huevos como una estrategia de conservación sustentable.

Olive Ridley Sea Turtles (*Lepidochelys olivacea;* Eschscholtz, 1829) are listed as a vulnerable species on the IUCN Red List and are considered to be in overall global decline (Abreu-Grobois and Plotkin, 2008). Population studies indicate this species to be most abundant in the Eastern Tropical Pacific; however, quantitative estimates of abundance are uncertain because of difficulties in estimating the number of females in mass nesting events (also known as arribadas) and large interannual fluctuations in nesting abundance that characterize this species (Valverde and Gates, 1999; Cornelius et al., 2007; Eguchi et al., 2007; Valverde et al., 2012).

The Ostional National Wildlife Refuge (ONWR) was established in Costa Rica in 1983 to protect the Olive Ridley Sea Turtle rookery (Campbell, 1998), which supports a nesting female subpopulation, once estimated to contain ~134,400 females (Abreu-Grobois and Plotkin, 2008). Within ONWR, the Nosara and Ostional beaches extend 7 km with variable width. The majority of sea turtle nesting activity at ONWR is concentrated at Ostional Beach, which is one of the most important Olive Ridley nesting sites in the world (Cornelius, 1981). In the early 1980s, the arribadas at Ostional contained between 35,000 and 180,000 nesting females (Cornelius and Robinson, 1981, 1983). More recent estimates indicate that this subpopulation may reach up to 470,000 over a period of up to 7 d of oviposition (Valverde et al., 2012). The difference between these estimates supports the need to test and validate alternative standardized methodologies for estimating arribada abundance.

The Ostional nesting aggregation also supports a large-scale community-based egg harvest program, in which approximately 20% of the eggs laid during each arribada are harvested by the local community for commercial use (Valverde et al., 2012). The legal harvest of sea turtle eggs by the local association takes place within the first 36 h of each arribada (Campbell, 1998). The socioeconomic success of the egg harvest program so far has made it a potential model for community-based conservation at other mass nesting beaches (Ballestero et al., 2000; Campbell et al., 2007).

Despite the importance of Ostional Beach as an arribada rookery, there are limited published data for this nesting beach since its discovery in 1970 and the legalization of the egg harvest in 1987 (Richard and Hughes, 1972; Campbell, 1998). This information deficiency has been attributed, in part, to methodological difficulties associated with generating robust and reliable estimates of arribada abundance (Campbell, 1998;

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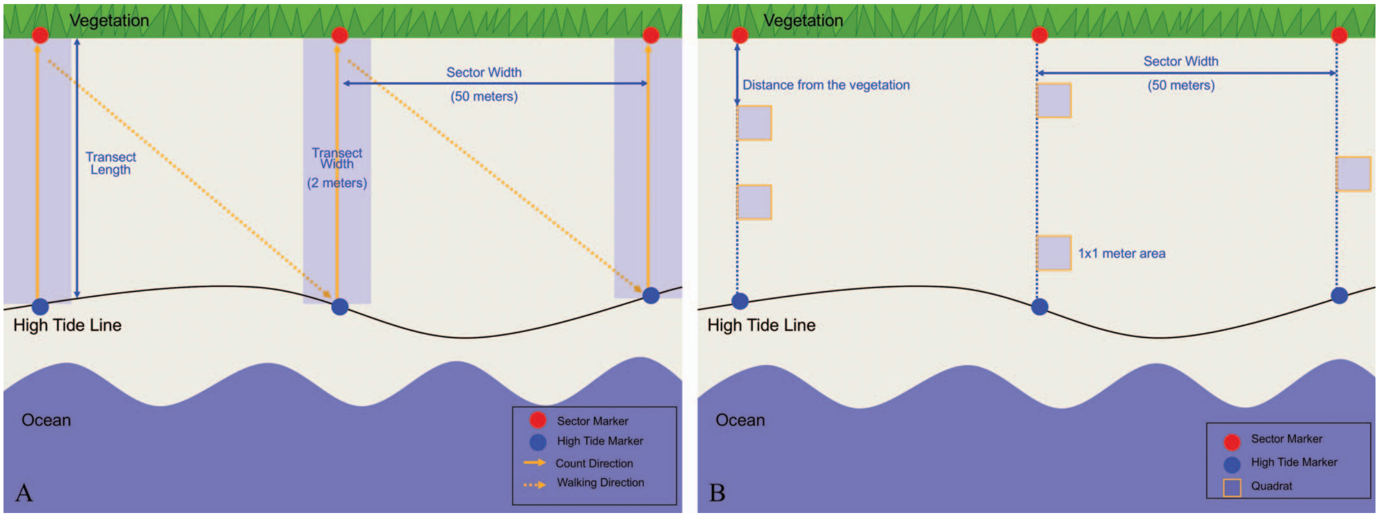

FIG. 1. Diagram of the (A) transect and (B) quadrat methodology as implemented in this study.

Ballestero et al., 2000). Monitoring various aspects of the nesting population at Ostional Beach (e.g., nesting female abundance, hatching success, and clutch densities) is critical to inform the effective management of the egg harvest program so it can continue to serve as a source of income for the local community (Campbell et al., 2007; Valverde et al., 2012).

Long-term monitoring of various parameters with the use of standardized and statistically robust methods is critical for providing managers with information that can be used to evaluate the status of this nesting subpopulation in comparison to historical data. A logistically practical and statistically robust methodology was developed to estimate arribada abundance at beaches around the world with the use of a "strip transect in time" technique (Gates et al., 1996; Valverde and Gates, 1999). This transect methodology estimates the number of egg-laying females and, therefore, the number of nests deposited during each arribada; however, this approach provides no information on the number of nests left in the sand following intraspecific clutch destruction and the collection of clutches by the egg harvest program on Ostional Beach. Previous studies at Ostional and other arribada beaches in Costa Rica report low hatching success (~8%) and have identified clutch density, rainfall, and incubation temperature as important factors affecting hatching success at arribada beaches (Cornelius et al., 1991; Honarvar et al., 2008; Valverde et al., 2012). Additionally, a recent study found a positive correlation between cumulative clutch density and clutch destruction at an arribada beach and recommended the long-term monitoring of clutch density and nest destruction at arribada beaches (Ocana et al., 2012). Several different methodologies, including quadrat sampling and simulations, have been used to estimate clutch densities at arribada beaches (Cornelius et al., 1991; Honarvar et al., 2008; Ocana et al., 2012). Therefore, we implemented an additional methodology with the use of quadrat sampling to provide another estimate of the clutch density and reproductive potential. Simultaneously implementing both methodologies provides a different perspective through a comparison of the estimated reproductive output with the estimated abundance of nesting females resulting from the current transect methodology.

Our data analyses allow us to generate an alternative estimate of the reproductive output, (while providing a measure of the magnitude of clutch destruction that occurs during each arribada), and provide a comprehensive assessment of the reproductive cost of this mass nesting behavior resulting from intraspecific clutch destruction, egg harvest, and predation at the nesting beach. Estimating these factors and their potential effects on the status of the nesting aggregation supplements the data needed for the continued monitoring of the nesting beach and the egg harvest program at Ostional.

MATERIALS AND METHODS

Study Site.—This study was conducted between September 2010 and April 2011 at Ostional Beach within the Ostional National Wildlife Refuge (ONWR), located on the Pacific coast of the Nicoya Peninsula in Costa Rica (9.996471°N; 85.697800°W). Nesting turtles typically are more abundant during the rainy season (May through November), and the beach structure is highly dynamic, given that nearby estuaries often overflow and cause substantial erosion. The beach is marked with sector markers every 50 m from north to south. The village of Ostional is located adjacent to the main nesting beach at Ostional Beach, where arribadas tend to concentrate (Valverde et al., 2012).

Arribada Census.—Nesting turtle abundance in a given arribada was estimated with the use of strip transect in time methodology following the guidelines from Gates et al. (1996) and Valverde and Gates (1999). Arribada census data through December 2010 were published in Valverde et al. (2012); data for January through April 2011, however, are presented here for the first time. Briefly, transects were set up after the first night of each arribada by placing transect markers at the high-tide line in front of each sector marker. Markers were placed where the current arribada was concentrated and along either side of the beach until nesting tapered off. We censused transects every 2 h during the peak nesting activity (>100 nesting females) of each arribada by walking from the high-tide marker to the sector marker and counting the number of nesting females with eggs present in the nest chamber that fell within the 2-m width of the transects (Fig. 1A). Censuses were conducted each night until all transects produced no counts, at which point the arribada was considered to have ended. We analyzed transect results with the use of the

Arribada Portal web application to estimate the number of egg-laying females in each arribada (Valverde et al., 2012).

Clutch Density Census.—Within 3 days following the conclusion of each arribada, we randomly placed 50, 1 × 1 m quadrats within the same area where transects were performed (Fig. 1B). We randomly selected quadrat locations with a random number generator to designate sector numbers (the area directly in front of the sector marker) and distances from the vegetation as coordinates for the top left corner of each quadrat. Quadrats were constructed with the use of PVC pipes strung together with a 4-m-long string. This collapsible and portable frame ensured the dimensional congruency of all quadrats. We excavated each quadrat to 60 cm in depth to count the number of clutches found within the quadrat. We counted clutches not entirely within the quadrat only if they overlapped with one of the two marked sides of the frame. We distinguished between clutches that were adjacent to one another based on the average number of eggs per clutch for each arribada, and by identifying the elliptical perimeter of each nest cavity, characterized by an abrupt transition between compact and loose sand.

To distinguish between newer and older clutches, we conducted a preliminary study on 10 clutches to determine the changes in egg features over time. We marked each clutch after it was laid and carefully excavated the perimeter of the clutch on each of the first 10 days of incubation to observe white spot development as described by Chan (1989) and Miller (1985). Briefly, the eggshell was creamy white and translucent when laid and a white spot formed at the top of the egg as it dried and absorbed water. The diameter of this white spot increased until the entire surface of the egg was opaque, after ~10 days (Miller, 1985). Additionally, we conducted clutch excavations (at the end of the incubation period) to increase familiarity with sea turtle egg features. This preliminary study allowed us to distinguish between newer clutches from the most recent arribada (10 days of age or less) and older clutches from previous arribadas (>10 days of age). Given that relatively few solitary nesters laid clutches along the entire expanse of the beach and that mass nesting events typically were preceded with periods of decreased nesting activity (Bézy, pers. obs.), quadrat estimates likely also excluded any solitary clutches that were located within the area of the arribada and remained intact following the conclusion of any arribada event.

To estimate the total number of clutches remaining on the beach, we extrapolated the counts of new clutches from the 50-m^2 sample area to the entire beach area where turtles concentrated each arribada, as determined from the transect censuses. We then compared total clutch abundance estimates from the quadrat methodology to the estimate of egg-laying females obtained from the transect method.

Statistical Analysis.—We fit the distribution of number of clutches per quadrat for each arribada event with the use of one negative binomial distribution or a mixture of two negative binomial distributions by maximum likelihood. We performed a choice between both models with the Akaike Information Criterion (Akaike, 1974). We conducted a power analysis to determine whether the sample size of quadrats was adequate by using a bootstrap resampling of observed data (Efron, 1981). For each arribada event, we established mean clutch density by simulating the total effort from 50 quadrat excavations (current effort) to a single excavation, producing 1,000 simulations each time. For each of these replicates, we obtained the number of clutches in the excavations randomly with replacement from the set of 50 observed values. We then calculated the mean and standard error of the number of clutches in the excavations for each combination of arribada event and effort.

All values are expressed as means ± SE. We analyzed mean new and old clutch densities by season (rainy and dry) using ANOVA, followed by a Bonferroni-adjusted LSD *a posteriori* test. The months of May through November were designated as the rainy season and all other months were designated as the dry season. We then compared extrapolated clutch abundance estimates based on the quadrat methodology with estimates of the total number of clutches laid based on the transect methodology by comparing the 95% confidence intervals ($CI_{95\%}$); only when confidence intervals did not overlap were clutch estimates considered significantly different.

Results

Seven arribadas occurred between September 2010 and April 2011. The only arribada not sampled (due to lack of personnel) occurred in the beginning of January 2011. We did not include data from the April arribada because $CI_{95\%}$ estimates by each method encompassed 0, making results unreliable. To ensure congruency in distinguishing between newer and older eggs, we created a table of descriptions including photographs for use as a guideline (Table 1).

The September and October data were best explained by a mixture of two negative binomial distributions but one distribution was sufficient to explain the observed data for November (Table 2). Fitting a mixture of two binomial distributions for January, March, and April data was impossible, because the number of clutches was lower. The power analysis revealed that approximately 30–50 quadrat excavations provided adequate estimates of the mean number of clutches and similar standard deviations for all arribada events (Fig. 2). The confidence interval width for 50 excavations falls within the range of confidence interval width for 30 excavations or more (Fig. 3).

New and old clutch density estimates were significantly different between the rainy and dry seasons ($F_{3,546} = 57.44$; $P > 0.001$) in agreement with a decrease in nesting turtle abundance, as estimated by the transect methodology (Figs. 4, 5). That is, in the rainy season, when nesting females were more abundant, there were significantly more new clutches than old ones (Fig. 4). The mean total clutch densities for the rainy and dry seasons were 4.41 ± 0.27 nests m^{-2} and 3.77 ± 0.22 nests m^{-2}, respectively. The mean clutch density for new clutches was 3.18 ± 0.78 and 0.41 ± 0.18 clutches m^{-2} for the rainy and dry seasons, respectively, and the mean clutch density for old clutches was 1.85 ± 0.20 and 3.36 ± 0.19 clutches m^{-2} for the rainy and dry seasons, respectively (Fig. 4).

Differences between the quadrat and transect estimates of total clutches laid for each arribada ranged from 0.04 to 52.6% (Fig. 5). Quadrat estimates tended to be lower than transect estimates, particularly in the rainy season when larger arribadas occurred. Estimates for the arribadas of September and October (>100,000 nesting females) were significantly different, as per the nonoverlapping confidence intervals on mean values for these months (Fig. 5). Estimates generated from each methodology for all other months did not differ significantly. We did not include results for the month of April in our analysis as these were not valid, because the confidence intervals spanned zero for both methods. This is likely because of the large variance per sample, characteristic of many small arribadas (<1,000 nesting females).

TABLE 1. Distinguishing features of the eggs from new and old nests at Ostional Beach, Costa Rica based on white spot development (Miller, 1985; Chan, 1989). The inside of the egg was ascertained only if an egg was accidentally broken upon excavation.

Type of nest	New	Old
Description	From the most recent arribada	From previous arribadas
Example photograph		
Egg features	•Presence of a white spot on top •Transparent coloration, with creamy white spots •Flexible, barely rigid shell •Yellow yolk within (if broken)	•White, opaque, and solid coloration (no spots) •Dense and rigid shell, under pressure •Presence of mold or insect larvae •Embryo present within (if broken)

DISCUSSION

As Honarvar et al. (2008) showed, hatching success at arribada beaches was inversely proportional to clutch density. The mean clutch density observed in this study (4.41 nests m^{-2}) was similar to the optimum clutch density (55.9% hatching success at 5 clutches m^{-2}) found in their study (Honarvar et al., 2008); however, overall mean hatching success at Ostional is reported between 0.0 and 32.6% (Valverde et al., 2012). Because the Honarvar et al. (2008) study cleaned the sand of broken eggs and fenced off experimental plots, clutch densities at Ostional may still be suboptimal, because the high organic matter content of the sand caused by intraspecific clutch destruction provides an optimal medium for microbial growth (Valverde et al., 2012). Microbial load may be just as important as clutch density in determining hatching success at Ostional, as this is correlated with increases in clutch destruction at higher densities (Cornelius et al., 1991; Clusella-Trullas and Paladino, 2007; Ocana et al., 2012).

The bimodal distribution of quadrat data shows that arribadas are not evenly spatially distributed, and instead produce areas of higher clutch density bound on either side by areas of low clutch density. This could be a strategy in which nesting females aggregate spatially across the beach to reinforce the predator satiation technique (Eckrich and Owens, 1995), by producing a central area of higher clutch density. The distribution of arribadas further stresses the importance of appropriately adjusting the location and span of both transect and quadrat counts for each arribada, rather than using a fixed survey area (Valverde and Gates, 1999).

By calculating the difference between transect and quadrat estimates and factoring in reported egg harvest rates, we can generate an estimate of the magnitude of clutch destruction (= number of clutches removed from the beach prior to completion of the incubation period), for each arribada. Clutch destruction was highest in September (52.6%) and October (22.6%) when arribadas were particularly large and the differences in transect and quadrat estimates were high, while the harvest was a relatively small percentage (<2%) of the total number of clutches laid during this time period (Valverde et al., 2012). The results from our study are consistent with historical data on clutch destruction and harvest rates in that the proportion of clutches that remained on the beach was highly variable, depending on the size and season of the arribada (Cornelius et al., 1991; Ballestero et al., 2000; Valverde et al., 2012). The positive correlation between clutch loss and arribada size observed in our study is similar to that observed in previous studies (Cornelius et al., 1991; Ocana et al., 2012). Our clutch loss estimates for the September arribada are much higher than those previously reported for arribada beaches (Cornelius et al., 1991; Ocana et al., 2012), likely because arribada abundance also vastly exceeded those previously observed.

Hatchling production estimates for each arribada in the rainy season can be generated by combining the total number of clutches estimated with mean clutch size (98.89 eggs; Valverde et al., 2012) and hatching rates (8.3%; Cornelius et al., 1991). Given that a total of ~462,380 nests remained on the beach for the September, October, and November arribadas combined, the results from our study indicate that an estimated 3,795,000 hatchlings were produced during those arribadas. Hatching

TABLE 2. Model selection for the number of clutches per quadrat. A mixture of two binomial distributions cannot be fitted for January, March, and April data because of the lower number of clutches. The underlined value for AIC indicates the selected model. NB is negative binomial.

Arribada month	AIC for one NB distribution	AIC for two NB distributions	ΔAIC	Akaike weight of selected model
September	239.1	231.0	8.079	0.98
October	245.1	244.2	0.837	0.60
November	185.6	186.8	1.192	0.64
January	120.9	–		
March	80.9	–		
April	41.5	–		
Global	669.7	662.0	7.723	0.98

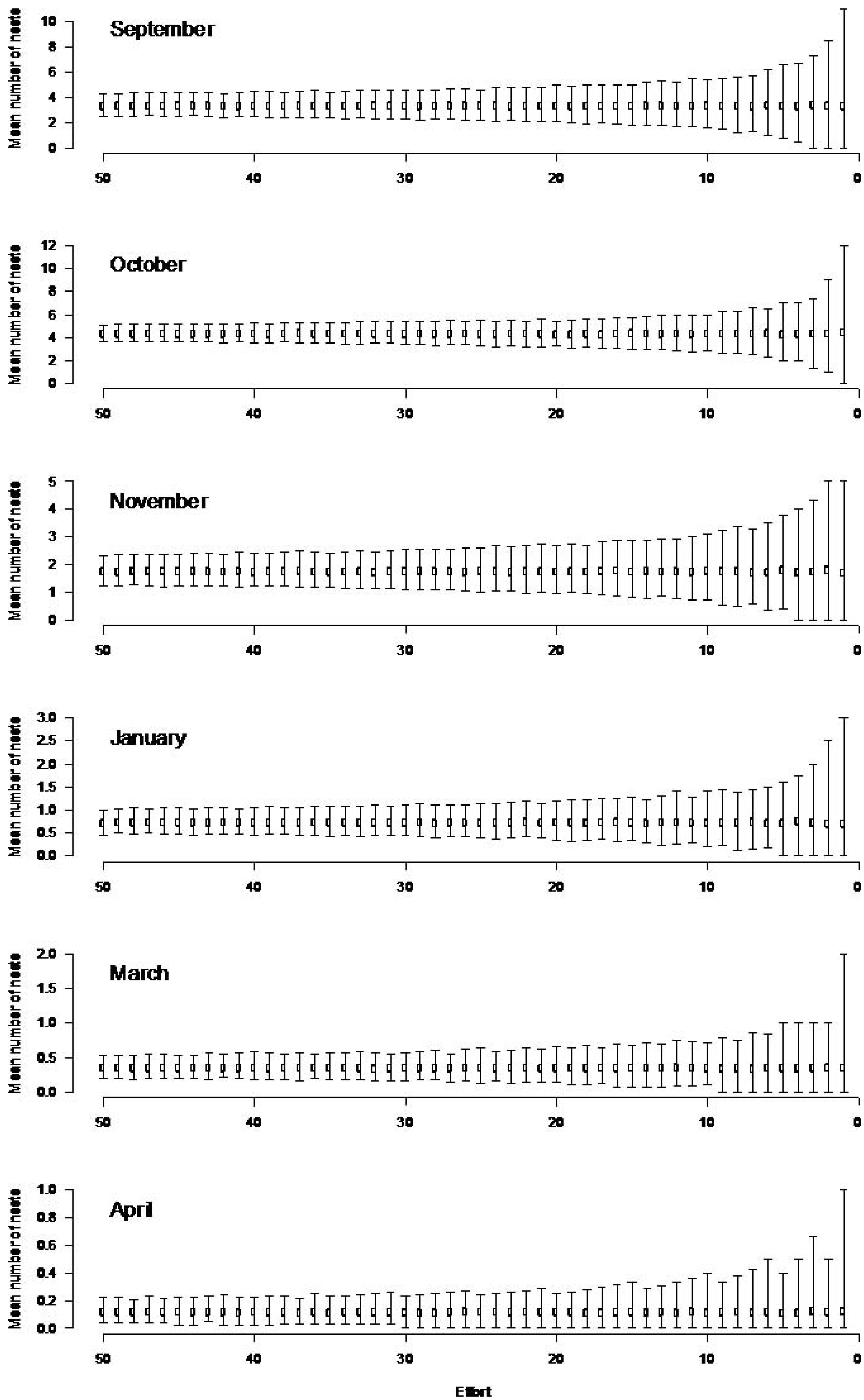

FIG. 2. Power analysis varying the effort of sampling from 50 excavations (current data) to 1 for each arribada event. Error bars represent a 95% confidence interval (2.5–97.5% quantiles). The y axis is the mean number of clutches per excavated plot.

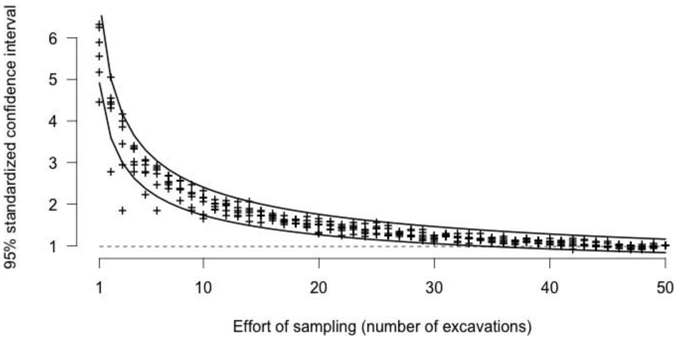

FIG. 3. Ninety-five percent confidence intervals (standardized by the confidence interval for 50 excavations) as a function of the sampling effort (number of excavations). The two plain lines represent the 95% confidence interval of the linear log-log fit of the data. The dashed line shows the average confidence interval for 50 excavations.

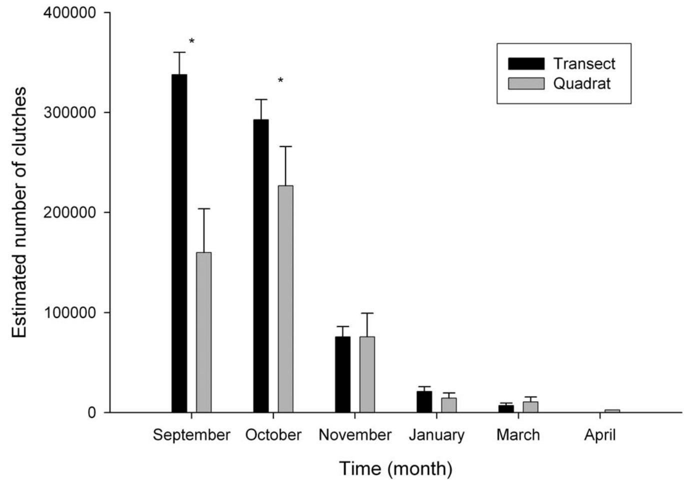

FIG. 5. Comparison of estimated number of clutches ($\pm CI_{95\%}$) based on the transect and quadrat methodologies for each arribada at Ostional Beach, Costa Rica. Rainy season arribadas occurred September through November of 2010; dry-season arribadas occurred January through April of 2011. Nonoverlapping confidence intervals indicate that means are significantly different (indicated by asterisks). Transect estimate data for September through December 2010 are published in Valverde et al. (2012).

success in the dry season is near zero, and these months, therefore, are not likely to contribute a large proportion of the overall hatchling production for Ostional (Valverde et al., 2010, 2012). For illustration purposes, if we assume that 1 in 1,000 hatchlings survives to adulthood (Frazer, 1986), estimates from this study suggest that ~3,795 hatchlings would reach sexual maturity (Valverde et al., 2010). Further studies are required to determine whether the current hatchling production at Ostional is sufficient to maintain current population levels, especially because age class-specific mortality rates are unknown for this population.

Overall, the simultaneous use of both count methodologies provides a feasible and statistically robust way of estimating clutch density, hatchling production, and clutch destruction over time through comparisons between estimates, reproductive, and egg harvest data. Although the transect method provides a good estimate of the number of clutches laid, it does not account for the amount of clutches harvested and those destroyed by other nesting turtles. Furthermore, transects typically are not set up until the day following the first night of an arribada, given that arribadas tend to shift in spatial distribution. Because of this, an unknown proportion of nesting females from the first night of the arribada is left unaccounted for within the transect estimate. Therefore, the larger difference between estimates from each methodology in the rainy season is most likely caused by increases in intraspecific clutch destruction at higher densities (Cornelius et al., 1991). On the other hand, the smaller magnitude in abundance and more abrupt timing (i.e., shorter duration, faster buildup and end) of arribadas during the dry season leaves a larger proportion of the total clutches laid unaccounted for (from the first night of the arribada) within the transect estimates for this season. Therefore, the quadrat methodology provides a different measure of the reproductive output, which takes these other factors into account and provides an estimate of the effective clutch density following each arribada. Although both transect and quadrat methodologies should preferably be used simultaneously, each could also be used individually to target either nesting population estimates or reproductive output. Although the transect methodology requires more personnel and longer hours to perform counts, the quadrat methodology is more feasible when fewer personnel are available. Using both transect and quadrat methodologies simultaneously, however, makes it possible to compare results and to observe changes in clutch density and the rate of clutch destruction over time.

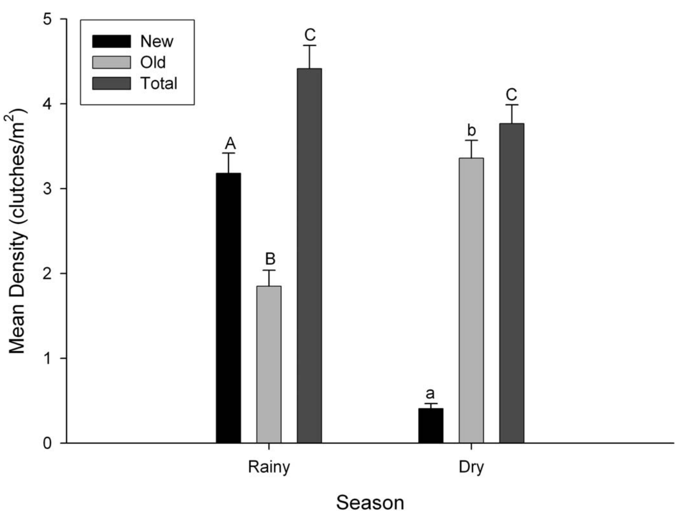

FIG. 4. Mean clutch density ± SE at Ostional Beach, Costa Rica of new and old clutches for the rainy season (May through November) and dry season (December through March). Seasonal means with letters of different case are significantly different according to the Bonferroni-adjusted LSD *a posteriori* test ($F_{3,546} = 57.44$; $P > 0.001$) for old vs. new clutches. Seasonal totals were not significantly different.

This novel comparison of methodologies provides a different evaluation of the status of the Olive Ridley nesting aggregation at Ostional with net clutch estimates, while evaluating the quadrat methodology as an alternate count method for arribada abundance estimates. Furthermore, this quadrat sampling method also can be used after the end of the incubation period for each arribada to conduct excavations and evaluate hatching success in the same areas that were surveyed for each respective arribada. The continued use of these methodologies can provide for standardized long-term monitoring of nesting abundance, clutch density, and hatching success at Ostional and other arribada beaches to inform management decisions.

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