

Mass nesting of olive ridley sea turtles *Lepidochelys olivacea* at La Escobilla, Mexico: linking nest density and rates of destruction

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ABSTRACT: Olive ridley sea turtles *Lepidochelys olivacea* exhibit synchronized nesting behavior that affects egg survival through a variety of mechanisms, including intra-specific nest destruction. This activity is difficult to quantify due to the frequency of arribadas (mass nesting events that occur over several days) and temporal overlap of incubation periods. We hypothesized that nest destruction is positively related to cumulative nest density. We quantified these variables through direct observation of nesting by 1293 turtles in 26 plots (each 9 m²) during 2 arribadas at La Escobilla, Mexico, in 2009. Cumulative nest densities ranged from 1 to 8 nests m⁻². The proportion of turtles observed destroying eggs was used as a proxy for nest destruction. A total of 5.12 and 23.10% of turtles destroyed eggs in the first and second arribadas, respectively. We used a mixed model logistic regression to determine that the odds of destruction (or the probability that a turtle destroys eggs divided by the probability that she does not) increased 21 % for every additional nest per square meter. We could not measure total egg survival as a function of nest density likely due to extreme weather conditions and beetle predation that resulted in 0% hatchling production over most of the study area in August to October 2009. However, understanding the relationship between nest density and the probability of nest destruction is an important first step toward quantifying density dependence in olive ridleys. We recommend that monitoring plans include standardized measurements of density (nests per square meter) and destruction levels to improve estimates of annual hatchling production.

KEY WORDS: Olive ridley sea turtle · *Lepidochelys olivacea* · Arribada · Density · Nest destruction · La Escobilla · Density dependence

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INTRODUCTION

Intra-specific density-dependent factors affect population dynamics in a variety of taxa (see Brook & Bradshaw 2006 for a review). Understanding the mechanisms that lead to density dependence is important for conservation of protected species because of the pressing need to develop scientifically sound approaches to increase abundance and distribution. Density impacts are demonstrated in aggregations of

nest-building taxa, such as salmonids and sea turtles, where high densities of females and nests can affect egg survival (Cornelius et al. 1991, Sandercock 1991, Honarvar et al. 2008). Density-dependent cohort production from aggregate nesting can ultimately lead to variability in population age structure and population cycles (Higgins et al. 1997).

Ridley sea turtles aggregate to form remarkable mass nesting events ('arribadas') that occur at only a few beaches worldwide. During olive ridley *Lepi-*

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dochelys olivacea arribadas, 1000s of females gather to synchronously nest over a few consecutive nights (and up to several weeks) (Bernardo & Plotkin 2007). The largest arribadas number from 10s to 100s of 1000s of turtles at La Escobilla (Mexico), Ostional (Costa Rica) and along the coast of Orissa (India) (Bernardo & Plotkin 2007). Arribada dynamics are complex, with many factors that may affect nest survival (Fig. 1). High nest density is believed to negatively impact nest success through interrelated factors, such as microclimate variations and likelihood of predation. One often observed factor is intra-specific nest destruction, which is defined as the damage of previously laid eggs by later-nesting females. In addressing the evolution of arribadas, Bernardo & Plotkin (2007) hypothesized a functional relationship between the probability of nest success and nest density in which a more or less exponential increase in nest destruction occurs with increasing nest density. Further, they theorized that predation trumps the role of nest destruction in driving nest mortality until high nest densities are reached, at which point destruction becomes a dominant factor. Investigating the relationship between nest density and each potential factor that could impact survival, such as those mentioned above, is the first step to understanding what ultimately determines nest success.

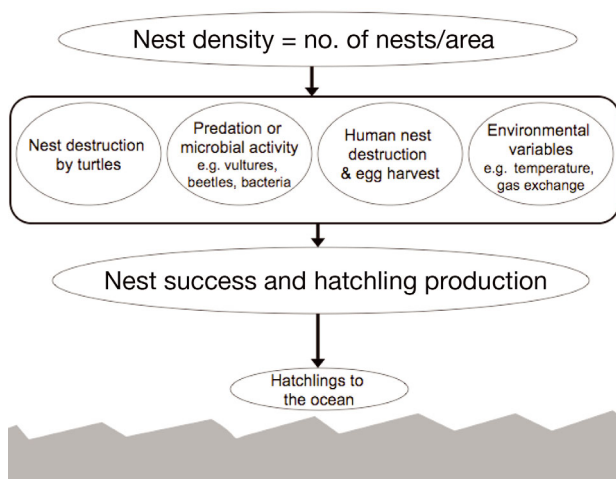


Fig. 1. Simplified diagram of factors affecting productivity at olive ridley *Lepidochelys olivacea* arribada nesting beaches. Note that nest density may act on hatchling production via a number of potential routes, which, in turn, may affect each other. For example, nest destruction might increase microbial activity, which could affect oxygen gas exchange. The present study focused on the potential of high nest density to result in high levels of nest destruction (later-nesting females destroying eggs from previously laid viable nests)

Although Bernardo and Plotkin provided the above hypotheses, previously published studies have not jointly examined intra-specific nest destruction and nest density at arribada beaches, perhaps owing to the difficulty of working with turtles *in situ* and quantifying nest density across space and time. However, previous research on sea turtle species at non-arribada beaches has examined the density–destruction relationship directly (Tiwari et al. 2006), and other studies have separately assessed the effects of either nest destruction or density at arribada (Cornelius et al. 1991, Honarvar et al. 2008) and non-arribada beaches (Bustard & Tognetti 1969, Girondot et al. 2002, Caut et al. 2006, Tiwari et al. 2010). For example, density-dependent impacts on nests have been empirically demonstrated in artificially manipulated nesting conditions; significantly lower hatching success occurred in high-density plots compared to low- or medium-density ones, likely due to interactions with temperature and gas exchange (Honarvar et al. 2008). In a seminal study of arribada destruction, eggs from a higher percentage of marked nests were damaged in larger arribadas and nest destruction increased in each successive night of an arribada and with each subsequent arribada in the season (Cornelius et al. 1991). Further studies that quantify levels of destruction at varying densities could improve the science behind management decisions at high-density nesting beaches, especially ones that consider nest removal to reduce density impacts.

Given the complexity of arribada nesting and logistical challenges of monitoring waves of nesting females that arrive nightly, managers may encounter difficulties in identifying how to focus research efforts and which variables to measure. Currently, government researchers at La Escobilla, Mexico, estimate the total number of nests using the Gates-Valverde transect count method (Gates et al. 1996). With an estimated 1.16 million nests in 2009/2010 making it one of the largest arribada nesting populations in the world, La Escobilla is an ideal location to consider potentially density-dependent determinants of nest success. In the present study, we provide the next logical step and build on previous work by explicitly focusing on the relationship between nest density and nest destruction behavior by individual females. We tested the hypothesis that nest destruction is positively related to nest density by directly observing turtle behavior over the course of 2 arribadas, and quantified naturally occurring nest densities and destruction in space and time.

MATERIALS AND METHODS

Study site

La Escobilla is a 7 km beach located on the Pacific coast of Oaxaca, Mexico (Fig. 2). It is primarily utilized by olive ridley turtles *Lepidochelys olivacea* and the most frequently used nesting area is divided laterally into 100 m wide stations with markers every 50 m. The beach is part of a national sanctuary that has been monitored by the Mexican government since 1967 (Marquez et al. 2001). Despite the beach's remoteness, there is considerable activity by various groups of people: biologists and volunteers with the Mexican Sea Turtle Center, armed Marines and government law enforcers, community members, and poachers illegally harvesting eggs. Aside from illegal egg harvest, other potential causes of nest failure at

this site include predation (e.g. dogs, vultures, beetles, crabs), water inundation (particularly in areas near the estuaries), extreme environmental conditions (e.g. high temperature, low humidity), and the aforementioned intra-specific nest destruction (E. Albavera pers. comm.).

Nesting data collection

Field work was conducted to monitor nesting between August and November 2009. Turtles nested during 2 study arribadas: August 14 to 18, 2009 (first arribada) and August 27 to September 4, 2009 (second arribada). Prior to the arribadas, 26 plots (9 m² each, 3 × 3 m) were constructed in pairs over a lateral distance of roughly 1.75 km (between Stns 8 and 25.5). Since the exact location of arribada nesting

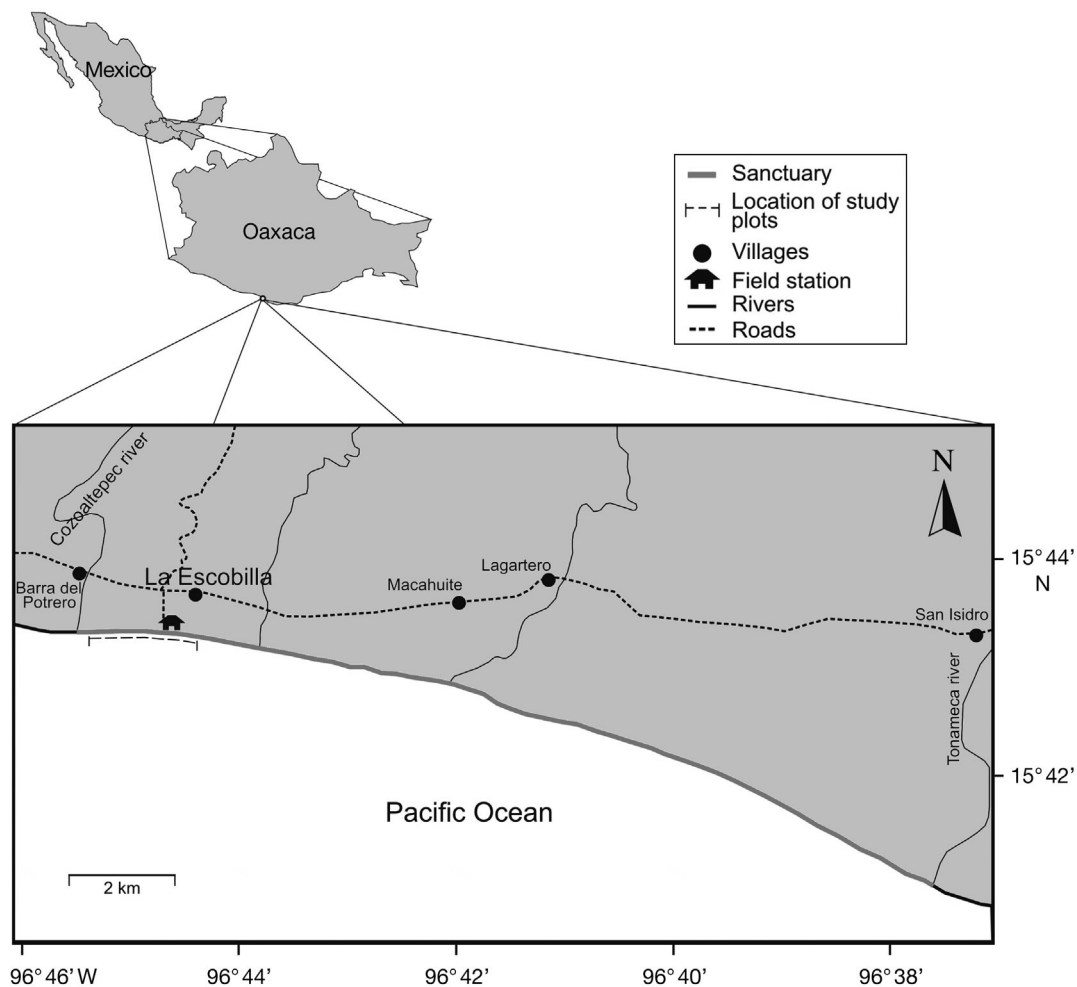


Fig. 2. Map of La Escobilla nesting beach, Mexico. Broken line indicates area of beach where study plots were located. The building symbol indicates the location of the Mexican government-sponsored field station. Map by E. Albavera, Centro Mexicano de la Tortuga

shifts, we located plots along the mid-beach of the most frequently used nesting area to increase the likelihood of plots being used during the arribada. Plots consisted of 4 corner posts with metal fencing that could be rolled open or closed to block nesting after the arribadas. We used large-linked fencing to allow any hatchlings from prior nesting to exit the plots. While it is possible that solitary nesters may have nested in plots, we believe that there were no nests in the plots at the start of the study, based on observational records at the beach. Any solitary nests that occurred during the days of the arribada were noted by observation of females' tracks and counted during our initial plot observation. After the first arribada, which lasted 5 nights, we fenced plots to prevent potential nesting by solitary females. We reopened plots 9 nights later, during the second arribada, and then re-fenced the plots after 8 nights. Because arribada nesting occurred fairly regularly between 22:00 and 06:00 h, we refer to each 24 h period as a 'night,' though some prefer 'session' (Valverde et al. 1998).

Following the conventions of other arribada researchers, we began data collection in study plots once 1000 females were observed on the beach during All Terrain Vehicle (ATV) surveys (Peralta et al. 2008). Each team member was assigned to monitor 5 to 6 plots every half hour, and turtle behavior was categorized by nesting activity: excavating, egg laying, covering, and evidence of nest destruction. Nest destruction was defined as observing a female unearthing eggs, or laying or covering her nest amidst freshly broken eggs. Because the entire nesting process takes about 1 h (E. Albavera pers. comm.), the team observed every turtle present in study plots. Females were marked with chalk, and diagrams of female locations were drawn to avoid double-counting the same nesting activity. Observation stopped for the night when there was a marked drop in the number of females. Plots were not fenced at the end of each night because arribada nesting did not occur during the day.

Towards the end of the incubation period, which often lasts around 45 d, the fence links were blocked with netting and plots were observed for presence of hatchlings.

Data analysis

Nest density in each plot was extrapolated from behavioral observations using methods similar to those of Cornelius & Robinson (1985). At the mo-

ment of data collection, some females had clearly nested, but others were observed excavating and had not yet laid a nest. Females commonly abort partially dug nest cavities due to external disruption or site unsuitability (E. Albavera pers. comm.); this results in incomplete nesting. Previous research at La Escobilla, conducted with similar levels of turtle–observer interaction and during a similar time of year as our study, found that 25% of females who began digging did not complete nesting ($n = 791$, over 3 separate arribadas and years) (Albavera & Karam 1999 and P. E. Albavera & M. S. Karam unpubl. data). Thus, in the absence of visual nest confirmation (subsequent observation of the nest or the same female covering a nest), the number of females observed excavating a nest cavity was adjusted downward by 25% to estimate the number of nests actually laid. We totaled the number of nests observed and estimated (from excavating females) to determine nest density per plot.

Nest density was quantified as the cumulative value of all the nests in the ground in each plot at the end of any given night. Thus, for the second arribada studied, nest density is the total number of nests present in each plot at the end of the first arribada plus the new nests added during the second arribada. To facilitate comparison across studies, we also report densities measured as nests per 9 m².

Nest destruction was evaluated at the turtle- and plot-levels (e.g. the number of females that destroyed eggs per plot), but not at the nest- or egg-level (e.g. the number of eggs destroyed per nest), due to an inability to accurately count destroyed eggs and identify the nest from which the eggs came. The presence of eggs on the beach surface was interpreted to mean that at least one nest was negatively impacted. 'Percent destruction' was calculated nightly and over the entire arribada by dividing the number of turtles that unearthed eggs by the total number of turtles present per plot, multiplied by 100. We have observed that a female destroys those previously laid individual eggs in her path, rather than entire nests, as she excavates her new nest cavity. Thus, we did not interpret destruction as a net loss of a nest and, therefore, did not change nest density as a function of observed (partial) destruction.

We compared nest density and nest destruction in the second arribada, during which destruction occurred on nests accumulated from both arribadas, and not in the first arribada, which had relatively little destruction. We initially calculated the correlation between the percent of females destroying eggs per plot across all nights of the arribada and the cumula-

tive nest density per plot. However, because we had complete individual-level data (a dichotomous measure of whether or not each turtle destroyed eggs), we ran a logistic regression to make full use of all of the information collected. Using R 2.10, we ran a mixed-model logistic regression in which we used nest density at time of nesting to predict the odds of a given female destroying eggs at that time. The odds of destruction are calculated as the probability that a given turtle destroys eggs divided by the probability that a turtle does not destroy eggs; changes in the odds of destruction are positively, but not proportionally, related to the probability of destruction. The fixed-effects model formulation was: $\text{Logit}(\text{destruction}) = \text{intercept} + \text{nest density}$. Plot was entered as a random factor to determine the effect of nest density on the probability of nest destruction at an individual turtle-level. This mixed-model approach accounts for variability in the probability of destruction attributable to random effects of plot selection by turtles (Raudenbush & Bryk 2002).

We placed one ibutton temperature data logger (Maxim Integrated Products) at nest depth alongside each plot to monitor ambient sand temperature every 2 h ($n = 22$ recovered). The values obtained represent estimates for a 45 d incubation period, as loggers were buried and nests were laid over a period of a few days.

We also excavated areas to evaluate the outcomes of second arribada nests (methodologies developed

by Centro Mexicano de la Tortuga; Miller 1999). Nests were located by probing the sand with a pole every 10 cm to find air pockets. Predation by beetles was noted and is clearly distinguishable by shell mastication. We excavated 5 entire 9 m² plots, as well as 1 m² samples in the other 21 study plots. Volunteers and researchers excavated an additional thirty 1 m² samples outside of the study area.

RESULTS

Our methods of direct observation in study plots were successful and a wide range of nest densities was observed (Table 1). Cumulative nest densities were quantified to account for destruction occurring on nests laid during both arribadas (Fig. 3). The second arribada had a significantly larger proportion of nest destruction than the first ($z = 8.928$, $p < 0.0002$), likely due to the increase in nest density per plot. There was a reasonable positive correlation between cumulative nest density and percent destruction (aggregated over all nights) per plot for the second arribada (Fig. 4; $r = 0.468$, $p = 0.016$). Using an estimated 45 d incubation period, over half of the nests' incubation periods overlapped, as there were only 9 d between arribadas. Nests would have additionally been impacted by a subsequent third arribada, if not for the fenced study plots (Peralta & Peñaflores 2010).

Table 1. Total turtles present, estimated nest densities per 9 m² plot ($n = 26$ plots), and occurrence of intra-specific nest destruction during 2 arribadas from August to September 2009 at La Escobilla, Mexico. Nest densities are reported as both new nests laid and as cumulative nests over the 2 arribadas. For nests damaged, the numerator is the number of times that distinct nesting females were observed destroying eggs divided by the total number. It is possible that eggs observed being destroyed are from multiple nests or that the same nest could be impacted more than once. Here we interpret observation of egg destruction to indicate that one viable nest was damaged. Mean destruction per night was weighted by sample size (numbers of females present per plot)

Variable	First arribada	Second arribada
No. of turtles per 9 m² plot		
Mean (SD)	21 (8)	28 (11)
Range	7–41	8–53
Nest density per 9 m² plot		
Mean (SD)	18 (6.76)	New: 24 (9.67); Cumulative: 42 (4.67)
Range	6–32	New: 5–46; Cumulative: 14–73
Nest destruction		
Estimated nests damaged, %	6.09 (29/476)	Cumulative nests: 15.30 (168/1097) Cumulative females and nests: 17.96 (197/1097)
Turtles destroying eggs, total %	5.12 (29/566)	23.10 (168/727)
Turtles destroying eggs (range of means per night, %)	0–15.12	6.97–28.57

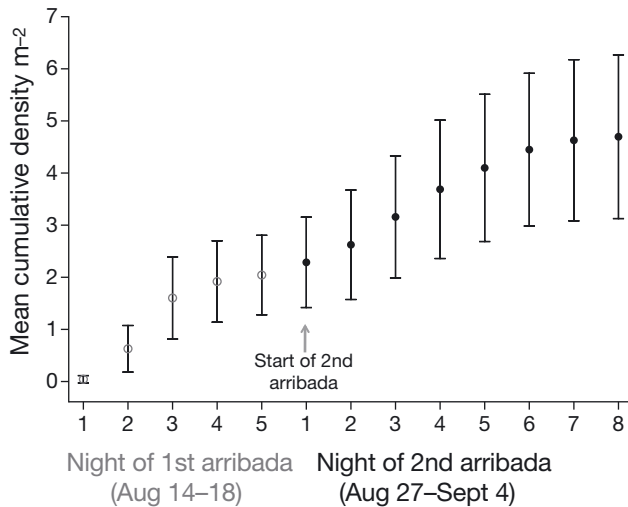


Fig. 3. *Lepidochelys olivacea*. Mean cumulative density of nests per m^2 (\pm SD) per night, counted in 26 plots over 2 arribadas. Cumulative densities were quantified to account for destruction of eggs occurring in nests from either arribada. Each data point is the mean density across all plots for a given night, and 1 SD is calculated over the mean. n (nests) = 476 (first arribada), 621 (second arribada), 1097 (cumulative total)

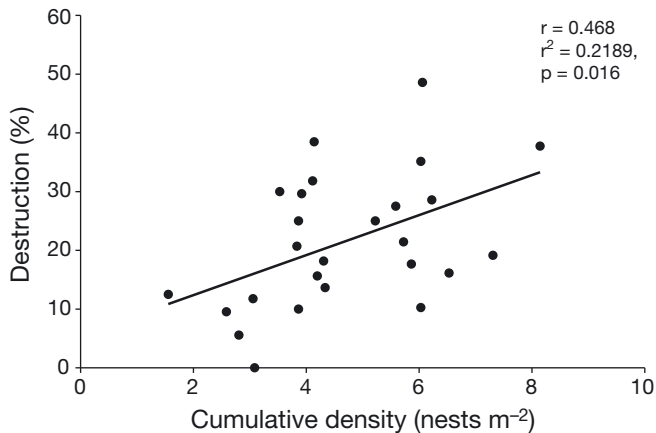


Fig. 4. *Lepidochelys olivacea*. Cumulative nest density (nests m^{-2}) and percent destruction aggregated over the second arribada. Each data point represents a 3×3 m plot ($n = 26$ plots). Percent destruction is the number of turtles that were observed digging up eggs divided by the number of turtles nesting over all nights of the second arribada. A linear trend line illustrates the positive relationship

A mixed-model logistic regression with plot entered as a random factor revealed a negligible effect of plot on odds of destruction (plot intercept = 8.4×10^{-12}), suggesting that any effect of density on destruction was consistent across study plots. The fixed-effects portion of the model had an intercept of -2.389 (SE = 306, $z = -7.817$, $p < 0.001$). We found a positive and statistically significant effect of nest

density in predicting the odds of destruction ($\beta = 0.191$, SE = 0.068, $p = 0.005$). Odds can range from zero to infinity and the odds of destruction are $p(\text{turtle destroys eggs})/p(\text{turtle does not destroy})$, where $p = \text{probability}$. The change in odds of destruction predicted by a 1 nest increase in density (m^{-2}) was calculated by taking the exponent of the beta coefficient for density (0.191); the odds that an individual turtle destroys eggs increases by 21% for every additional nest in the ground per square meter (95% confidence interval: 6 to 38%). Using values near the average cumulative density per plot as an example, our findings predict that at a density of 4 nests m^{-2} , the odds of a female destroying eggs would be approximately 1 to 5. At a density of 5 nests m^{-2} , the odds of destruction increase by 21% to 1 to 4.2.

Unfortunately, no hatching occurred in the area of beach chosen for our study, and none of our 26 plots had successful hatching, precluding us from estimating the effects of density on egg survival. All nests sampled in the study plots had evidence of beetle predation ($n = 215$). Outside of the highly used mid-beach study zone, 19 out of 30 nests sampled had evidence of successful hatching and 20 out of 30 had evidence of beetle predation. We do not report hatching success because it was difficult to determine numbers of eggshells due to fragmentation from predation. Temperature data loggers revealed mean temperatures per plot (using a 45 d estimation of incubation period) of 34.6°C (SD = 0.68) and 35°C (SD = 0.69). A mean of 23 and 30 d reached 35°C in the first and second arribadas, respectively, across all loggers.

DISCUSSION

We successfully quantified nest densities and destruction levels of olive ridley turtles *Lepidochelys olivacea* during August and September, when the largest and most frequent arribadas occurred at La Escobilla, Mexico (Albavera Padilla et al. 2009). The total number of nests estimated during the first and second arribadas (95% confidence intervals), respectively, were 186 269 (146 165 to 226 362) and 198 595 (136 107 to 261 082) (Peralta & Peñaflores 2010). Nest destruction (when nesting females damage previously laid eggs) was a frequent occurrence, with up to 28.5% of turtles destroying eggs per night in plots. More notable is the significant predictive effect of density, wherein nest density was positively related to the odds of a given turtle destroying eggs. It became clear in our investigation that frequent arrib-

adas and overlapping incubation periods preclude simple comparisons of impacts of nests (and turtles) on each other. Thus, the relative importance of factors that affect nests may depend on timing; this is especially true of destruction impacts, as the accumulation of nests from just 2 arribadas resulted in higher destruction levels than were evident after only 1 arribada.

Surprisingly, no hatching from the 2 arribadas (August to September 2009) was observed in the middle beach zone that was the focus of our study, including within our plots. Data collected from temperature loggers and nest excavation post-incubation suggested that predation by beetles and warm dry El Niño weather were primary determinants of nest failure. All sampled study area nests had evidence of beetle predation, indicating a major conservation concern at La Escobilla. Sand temperatures had consistently high mean maximums above the proposed 35°C lethal threshold for incubating olive ridley eggs (Valverde et al. 2010). The areas where hatching occurred outside the mid-beach zone were near high tide and estuaries that are likely to be cooler and have fewer beetles. Based on our observations, season, microclimate and arribada timing affect how prevalent any single factor will be in determining nest success. Because of this, we recommend monitoring a suite of factors.

Quantification of density-dependent effects is difficult and previous studies have used a variety of methods to evaluate nest density or destruction levels, depending on their goals (Table 2). Nest density is a dynamic value that changes as new nests are laid, which complicates our ability to evaluate it. This has led researchers to manipulate densities for study (e.g. Honarvar et al. 2008), to directly observe nesting activity in plots or transects (present study), or to excavate areas post-incubation (e.g. J. Jang unpubl. data). The latter method of density estimation can be difficult at arribada beaches where nests are often overlapping. We recommend that future studies quantify cumulative density, including all nests concurrently incubating, in the comparable unit of a square meter and aggregated by night, which can then be scaled up to an entire arribada if desired. In our study, cumulative values provided a more realistic picture of the quantity of nests in the ground. This is especially relevant given the nature of nesting activity at La Escobilla, with short time periods between arribadas: between 2001 and 2005, 26 arribadas had incubation periods that overlapped with 1 subsequent arribada, and 4 overlapped with 2 arribadas (Albavera Padilla 2005). Thus, true esti-

mates of nest densities should take into account the fact that incubating nests are impacted by multiple arribadas, including both inter- and intra-arribada destruction.

Given its prevalence during arribadas, we believe that destruction should be regularly quantified, especially when taking into account the secondary-effects on egg survival, such as potential promotion of microbial activity and decreased oxygen availability (Fonseca et al. 2009). We recommend a standardized measurement of destruction that can be compared among studies, i.e. a method that quantifies percent females observed destroying eggs during nest construction (e.g. Girondot et al. 2002, present study). This considers destruction as a probability based on individual turtle behavior or on a turtle-level. A nest-level approach is to tally marked nests that are destroyed (e.g. Cornelius et al. 1991), but it can be difficult, after the fact, to determine that a missing nest marker indicates destruction. Our methods required many human resources because we identified all destruction that occurred in our plots. We recommend future discussion of a representative way of extrapolating destruction levels from less frequent behavioral observations. In addition to standardizing methodologies, it is important to operationalize and clearly define 'nest destruction;' this term implies loss of an entire nest, but actually refers to individual eggs that are damaged. Although a hatchery study was conducted with artificial destruction (Caut et al. 2006), empirically obtaining specific egg-level destruction estimates remains a difficult undertaking *in situ* (Girondot et al. 2002). Further research at this individual egg-level would clarify reporting of destruction levels.

The lack of standardized methodology makes comparisons of our present findings with previous studies difficult. Despite these limitations, many of the estimates of nest density and destruction reported at other arribada beaches appear quantitatively similar to our findings (Table 2). Of particular interest is that Tiwari and colleagues found a significant relationship between nest density and destruction at a non-arribada nesting beach, using an analytical approach similar to ours (Tiwari et al. 2006). While densities are usually lower at non-arribada beaches, nesting models such as the above that examine spatial use by incorporating density-dependent factors could be a useful foundation for estimating hatchling production at arribada beaches. Behavioral observations, such as those reported here and in other studies (Table 2), are the first step towards quantifying population parameters for modeling.

Table 2. Summary of recent field studies of density and/or destruction during sea turtle nesting. Studies are grouped by how data were collected during nesting by females (passive studies or manipulated densities). For each study the following information is given: common name of sea turtle species studied (leatherback: *Dermochelys coriacea*; green: *Chelonia mydas*; olive ridley: *Lepidochelys olivacea*), location, time (number of arribadas over which data were collected), methods (how density and/or destruction variables were measured), results (n: sample size of nests or females; empirical findings of interest rounded to the nearest tenth—percent nests impacted by intra-specific destruction, percent females observed destroying eggs), and sources of data. 'Covering' refers to a subsequent nest laid overlapping the first nest and resulting in partial destruction of the 'covered' nest. CR: Costa Rica; arr.: arribada

Species	Location	Time	Methods	Results	Source
Passive studies					
Leatherback	French Guiana & Suriname	1994	Direct observation of percent females destroying eggs	n = 2356 females 21.1% females destroying eggs	Girondot et al. (2002)
Green	Tortuguero, CR	2000	Observation of nest densities and destruction from previous night in plots	n = 3081 nests 11% nests destroyed Probability (destruction) significantly increased with increasing density ^a	Tiwari et al. (2006)
Olive ridley	Nancite arr., CR	1981–1984 (a) combined over 8 arr. (b) 2 Aug 1981, 1982 arr. (c) Sep 1981–1984 arr. ^c	(a) Percent of marked nests destroyed estimated from aboveground presence of markers (b,c) Direct observation of percent females destroying eggs every 2–3 h in plots	(a) n = 422 nests 17.1% nests destroyed (b,c) sample size not stated (b) 11.4%, (c) 17.8% females destroying eggs ^b	Cornelius et al. (1991)
Olive ridley	Ostional arr., CR	1984 (a) Aug & Dec arr. (b) Aug arr. (c) Sep arr.	(a) Percent of marked nests destroyed estimated from aboveground presence of markers (b,c) Direct observation of percent females destroying eggs every 2–3 h in plots	(a) n = 200 nests 17.5% nests destroyed (b,c) sample size not stated (b) 22%, (c) 44% females destroying eggs	Cornelius et al. (1991)
Olive ridley	La Flor, Nicaragua	Sep 1999–Jan 2000	Compared hatching success of marked single nests versus nests with destruction	Higher hatching success in single nests ^c	Von Mutius (2000)
Olive ridley	La Flor arr., Nicaragua	2004–2005 3 arr.	Percent of marked nests destroyed in control plots	n = 886 nests 14.5% nests destroyed	Honarvar (2007, pers. comm.)
Olive ridley	Ostional arr., CR	1993	Random direct observation of nest destruction and excavation of nests	n = 2698 nests 7.8% nests destroyed	Madden et al. (2008, pers. comm.)
Olive ridley	La Escobilla, Mexico	2009 early and late Aug arr.	Direct observation of nest density and destruction in plots	n = 1097 nests 18% nests destroyed n = 1293 females 15.2% females destroying eggs	Present paper
Manipulated studies					
Leatherback	French Guiana	2002	Percent emergence success of covered/covering nests. Treatments: 50% eggs destroyed 25% eggs destroyed Control	n = 108 nests Covered/covering nests: 5% / 1.3% 8.8% / 1% 14.4% / 24.2% ^d	Caut et al. (2006)
Olive ridley	Nancite, CR	Nov 2005–Jan 2006	Hatching success in varying density plots: 2 (low), 5 (medium), 9 (high) nests m ⁻²	n = 80 nests ^e low 71.6%, medium 55.9%, high 29.5% Hatching significantly lower in high-density plots	Honarvar et al. (2008)

^aTiwari et al. also considered variation in the amount of beach disturbed by nesting females. ^bFor both Cornelius studies, only unweighted averages reported. Hatching success of marked nests reported for those that survived erosion, predation, and destruction. ^cAuthors state they found significantly lower mortality in single nests, but methods and results too difficult to interpret for comparison. ^dCaut et al. corrected emergence success to account for destruction. ^eNumber of nests not stated but interpreted based on number of plots of varying densities

From a population demography point of view, hatchling production is the ultimate variable to measure. Quantifying the effect of nest density on the probability of nest destruction is not only interesting

from an evolutionary perspective when considering this unusual reproductive behavior (Bernardo & Plotkin 2007), but empirically important for estimates of hatchling production and carrying capacity (e.g.

Tiwari et al. 2010). Our study fills a gap (Table 2) by addressing both nest density and destruction at arribada beaches. The next step we recommend is to build on our study by investigating the relationship of these variables to hatchling production and beetle predation. Observation of nest destruction has already translated into management action, such as legalized egg harvest at Ostional, Costa Rica (Campbell 2007), and ongoing research will help evaluate the impacts of such management.

In the past, large numbers of turtles at arribadas created a false positive perception of their conservation status (Cornelius et al. 2007). In reality, aggregate nesting has made olive ridleys vulnerable to a variety of natural and anthropogenic stressors, including intra-specific nest destruction and egg or adult harvest for human consumption. These 2 factors are linked; the main argument for controlled egg harvest is that eggs that would otherwise be destroyed by females can instead serve as an economic resource for local communities (Campbell 1998). Taking our example, the 1990 ban on sea turtle use in Mexico ended industrial harvest (Marquez & Carrasco-A 1996). The La Escobilla population has since increased remarkably to >1 million nests in 2000 (Marquez et al. 1996, NMFS/USFWS 2007). This quantity of nesting makes density-dependent factors more likely to influence overall hatchling production and determine future population size of this vulnerable species. After examination of previous studies that use a variety of methods, we have concluded that a standardized definition of nest density and destruction would help future comparability. Further studies will help determine the impacts of high nest density and destruction, provide scientific information to the discussion of sustainable egg harvest or other management options, and increase our understanding of potential mechanisms for improving the conservation status of olive ridleys. In the near future, quantifying density and destruction may be increasingly relevant for sea turtles at non-arribada beaches, where increased nest destruction as a result of decreased beach availability from sea level rise is a concern (Mazaris et al. 2009).

Acknowledgements. We kindly acknowledge funders for support of this project and of M. Ocana's graduate studies: AquaFish Collaborative Research Support Fellowship, British Chelonia Group, Vassar College Fellowships, Seaspace Inc., and Oregon State University's MANRRS Chapter and Dept. of Fisheries & Wildlife. We appreciate assistance from researchers at El Centro Mexicano de la Tortuga, especially C. Peñaflores Salazar, E. Albavera Padilla, and E. Peralta Buendía. We thank all the volunteers and community members who made field work possible, especially I. Bravo,

C. Thorstenson, J. Gutiérrez, A. Muñoz, and T. Huang. Thank you to Ezra Markowitz for help with this project. This manuscript was improved with helpful input from A. Evans and 4 anonymous reviewers. This research was conducted in accordance with institutional, national, and international guidelines, including approval from CONANP in Mexico and Oregon State University's IACUC.

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Editorial responsibility: Jeffrey Seminoff,
La Jolla, California, USA

Submitted: May 16, 2011; Accepted: October 3, 2011
Proofs received from author(s): December 27, 2011