UNIVERSIDAD DE COSTA RICA
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PATRONES INDIVIDUALES DE SELECCIÓN DE SITIO DE ANIDACIÓN PARA LA TORTUGA BAULA *DERMOCHELYS CORIACEA* (DERMOCHELYIDAE) EN TORTUGUERO, COSTA RICA

Tesis sometida a la consideración de la Comisión del Programa de Posgrado en Biología para optar al grado de Magister Scientiae en Biología

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A mis padres

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La tortuga baula, *Dermochelys coriacea*, se encuentra bajo peligro crítico de extinción (Sarti-Martínez 2000). Spotila *et al.* (1996) estimaron la población mundial de hembras adultas en 34,500 individuos, menos de un tercio del tamaño poblacional estimado para 1980. La población de baulas del Pacífico está disminuyendo rápidamente (Spotila *et al*. 1996, 2000), mientras que la del Caribe se estima que podría ser estable o estar disminuyendo lentamente (Troëng *et al*. 2004). Esta especie enfrenta una multitud de amenazas dentro y fuera del agua; las principales son: saqueo de nidos, captura incidental de hembras adultas (por redes y líneas de pesca) y contaminación oceánica y de playas (Chacón 1999, Sarti-Martínez 2000, Troëng *et al*. 2004). La protección de los nidos y de los neonatos puede compensar la mortalidad de adultos y traer estabilidad a algunas poblaciones de baulas en playas protegidas (Eckert y Eckert 1990, Dutton *et al.* 2005). En otras poblaciones, la disminución es tal que no puede tolerar siquiera niveles moderados de mortalidad adulta (Spotila *et al.* 1996). La población de hembras que anidan en playa Tortuguero, Costa Rica, se considera parte de la metapoblación del Caribe, que es una de las cuatro colonias anidadoras más grandes en el mundo luego de Guyana Francesa, Gabon y Trinidad y Tobago. (Chacón 1990, Tucker 1990, Troëng *et al.* 2004).

Para cada temporada de anidación de tortugas baula desde el 2000, la Caribbean Conservation Corporation (CCC) ha reportado nidos marcados que fueron destruidos por mareas (Cook y Troëng 2000, Reyes y Troëng 2001, Harrison y Troëng 2003a y b, 2004, De Haro y Troëng 2006). El caso extremo fue el 2002 cuando esto representó la mitad de los nidos marcados (Harrison y Troëng 2003a). Hasta ahora no se han reubicado nidos en Tortuguero porque no se puede predecir cuáles se perderían y cuáles no, específicamente en esta playa (Cook y Troëng 2000, Reyes y Troëng 2001). Sin embargo, Runemark (2006) estudió algunos factores en el éxito de eclosión de los nidos de tortuga baula en Tortuguero (entre 1998 y 2006) a nivel poblacional; encontró que los nidos colocados debajo de la línea de marea más reciente tienen éxitos de eclosión significativamente menores a los que son colocados encima de ésta, debido a una mayor mortalidad embrionaria. Entonces, Runemark (2006) sugiere reubicar estos nidos y monitorear su éxito de eclosión y periodo de incubación.

En general, la reubicación de nidos dentro de la misma playa (en vez de hacia un vivero) puede realizarse por diversos motivos tales como: altos niveles de saqueo, bajo éxito de eclosión en nidos naturales o alta pérdida de nidos por acción de mareas (Sarti *et al.* 1989, Eckert y Eckert 1990, Hall 1990, Chacón 1999, Reynolds *et al.* 2002). Esta estrategia se usa comúnmente dado que es relativamente fácil y barata, los nidos producidos tienen condiciones de luz y sustrato similares a un nido natural, no se necesita mucho personal ni recursos y la liberación de neonatos no debe ser monitoreada tan estrictamente como en el caso de viveros (Eckert & Eckert 1990, Dutton *et al.* 2005). Sin embargo, el reubicar nidos tiene costos asociados. Podría causar menos éxito de eclosión, aumentar el índice de embriones deformados o alterar los perfiles de temperatura y el tiempo de incubación, que afectan la proporción de sexos producida (Basford y Brander 1989, Eckert & Eckert 1990). Otro factor que se debe tomar en cuenta es la posible selección artificial que se estaría realizando al reubicar nidos, a favor de hembras de bajo valor adaptativo en cuanto a su selección de sitio (Mrosovky 1983).

La tortuga baula anida en playas arenosas tropicales y subtropicales cada 3-5 años (Sarti-Martínez 2000, Bell *et al.* 2003). Cada hembra anida hasta 11 veces por temporada (Bell *et al.* 2003). Según Mrosovsky (1983) la adecuada selección de sitio por parte de las hembras de tortuga baula depende de varios factores tales como: la accesibilidad a los sitios adecuados (dificultada por troncos, altas pendientes o un borde vertical de la playa), la visibilidad (dada por diferencia en la cantidad de luz) y la estabilidad de la playa.

La selección de sitio representa un intermedio entre anidar demasiado cerca del mar o demasiado cerca de la vegetación (Mrosovky 1983, Caut *et al*. 2006). Al anidar cerca de la vegetación se arriesga que el nido sea invadido por raíces (Caut *et al*. 2006), sufra desecación (Runemark 2006) o sufra índices mayores de depredación (Katilimis *et al.* 2006, Runemark 2006). También al aumentar al tiempo que la tortuga adulta y los neonatos se mantienen fuera del agua, aumenta el riesgo de que estos sean depredados o que se desorienten (Whitmore & Dutton 1985, Kamel & Mrosovsky 2004). Sin embargo, al anidar muy cerca del mar aumenta la probabilidad de que el nido sea arrastrado o lavado por mareas (Runemark 2006). Este segundo caso puede ser beneficioso para bajar la temperatura del nido y producir más machos (Runemark

2006), pero la influencia del agua de mar puede causar una mayor mortalidad por ahogamiento y toxicidad de cloruros (Whitmore & Dutton 1985, Caut *et al*. 2006).
Los patrones espaciales de anidación de hembras individuales de tortuga baula han sido tema de disputa. Algunos autores sugieren que las hembras tienden a dispersar sus nidos en diferentes ambientes y distancias de la marea alta para aumentar la posibilidad de que alguno se encuentre en un sitio adecuado (Carr & Ogen 1959, Eckert 1987, Tucker 1990, Sieg *et. al.* 2003, Kamel & Mrosovsky 2004). Esta dispersión de los nidos se debe a que suelen anidar en playas inestables donde es difícil predecir cuál nido será exitoso (Eckert 1987). También, una misma hembra puede anidar en varias playas por lo cual adapta su estrategia de anidación a una región en vez de una localidad específica (Kamel & Mrosovsky 2004, Runemark 2006).

Debido a los riesgos explicados anteriormente, tanto el reducido éxito de eclosión como la selección artificial que se puede ejercer, se debe evaluar si la reubicación de nidos es una opción viable de manejo. Esto se debe hacer tomando en cuenta las características de cada playa (Eckert & Eckert 1990).

El objetivo original del presente trabajo era reubicar los nidos mal colocados, según las indicaciones de Runemark (2006), y comparar los nidos reubicados con los naturales en términos de éxito de eclosión y diversas características de los huevos y neonatos. También se realizaría un análisis de los patrones de anidación que siguen las hembras en esta playa en cuanto a distancia de la marea alta y vegetación, y distribución a lo largo de la playa así como el éxito de eclosión y emergencia que obtienen de este uso. A partir de estos análisis se elaborarían recomendaciones relacionadas con la reubicación de nidos como una estrategia de conservación de la tortuga baula con el fin último de aumentar la producción de neonatos para la playa de Tortuguero, así como contribuir a mantener o aumentar la población.

El trabajo descrito anteriormente se realizó durante el 2007 y el 2008 en conjunto con los Asistentes de Investigación, participantes y Coordinadores de Campo de la Caribbean Conservation Corporation (CCC). Sin embargo, con el protocolo de reubicación utilizado solamente se logró reubicar cuatro nidos en el 2007 y ninguno en el 2008. Debido a que el número de datos obtenidos fue insuficiente para un análisis estadístico, no se logró hacer la comparación entre nidos reubicados y naturales, por lo cual en el artículo se presenta el análisis de patrones de anidación. En este análisis, no se encontró evidencia a favor de patrones individuales de anidación que sean repetidos para hembras individuales. Las hembras que incialmente anidaron en una zona expuesta a la marea no tendieron a repetir esta selección, lo cual rechaza la idea de que existan hembras que aniden mal consecutivamente. Además, no hubo una correlacion entre los éxitos de eclosión ni los de emergencia entre la primera y segunda observación. Se recomienda que el trabajo de reubicación de nidos se siga en un futuro, para determinar si es factible implementarlo como estrategia de conservación en Tortuguero.

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REVISTA DE BIOLOGIA TROPICAL – INTERNATIONAL JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

Individual patterns of nest site selection for the leatherback sea turtle *Dermochelys coriacea* (Dermochelyidae) in Tortuguero, Costa Rica.

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Abstract: Nest site selection for individual leatherback sea turtles, *Dermochelys coriacea*, is a matter of dispute. Some authors suggest a female will tend to randomly scatter her nests in order to optimize clutch survival in an unstable beach while others suggest that some site fidelity exists. Subsequent nest site selection and their hatching and emergence success were studied for Tortuguero beach, 1997-2008 (data gathered by Caribbean Conservation Corporation). Contingency tables were created for subsequent nest site selections using the previous nest site location as the column and the next nest location as the row, both for horizontal and vertical nest site selection. Also, hatching and emergence success between previous and next nesting events were correlated. Along the ocean-to-vegetation axis, Zone II or open sand was preferred (X^2=11.4, p=0.02, df=4). Along the coastline, a preference was found for Section 2, between mile markers 2 and 3 (X^2=26.5, p=0.048, df=16). No correlation was found between hatching success of subsequent nesting events (r=0.21, p=0.09, n=70), nor between their emergence success (r=0.19, p=0.12, n=70). In general, individual nest site preference corresponded with that found at a population level; a preference for open sand areas and mostly in the middle section of the beach. Poor nests sites, at risk of being washed out, were not chosen in the next nesting event. Given this, and the fact that no correlation exists between the success of subsequent nesting events, there is no clear proof of individual nest site selection playing an important role in overall nesting site preference for this species in Tortuguero. Further research, including data for the same females on different beaches, will shed more light on this issue. Continued cooperation and data sharing between organizations patrolling different beaches would facilitate further study.

Key words: leatherback, *Dermochelys coriacea*, individual nesting patterns, nest distribution, nest site selection

The leatherback sea turtle, *Dermochelys coriacea*, is classified as in critical danger of extinction (Sarti-Martinez 2000). Spotila *et al.* (1996) estimated the world population of adult females to be 34 500 individuals, less than one third of the estimate for 1980. The Pacific leatherback sub-population is rapidly diminishing (Spotila *et al*. 1996, 2000), while the Caribbean sub-population is thought to be either stable or slowly declining (Troëng *et al*. 2004). The population trend for this species has focused attention on conservation efforts on nesting beaches (Spotila *et al*. 2000). Nest relocation is a commonly used conservation strategy for this species (Eckert & Eckert 1990, Dutton *et al.* 2005) but doubts have been raised on whether or not it skews the gene pool for the species, by selecting for “bad nesters” (Mrosovsky 1983).

Leatherback females nest on tropical and subtropical beaches, every 3-5 years (Sarti-Martínez 2000, Bell *et al.* 2003). Each female may nest up to 11 times in a single season (Bell *et al.* 2003). Adequate nest site selection involves a balance between nesting too close to the high tide line, risking nests being washed out (Runemark 2006) and nesting too close to the vegetation, risking invasion by roots, as well as predation and hatchling disorientation due to artificial lighting on the beach (Caut *et al*. 2006, Katilimis *et al.* 2006, Runemark 2006).

It has been suggested that, since leatherbacks tend to nest on unstable beaches, some with considerable changes in tide and erosion levels (Eckert 1987) and move between different beaches (Whitmore & Dutton 1985, Runemark 2006), they will not select for specific sites but rather scatter their nests randomly in order to optimize clutch survival probability (Carr & Ogren 1959, Eckert 1987, Kamel & Mrosovsky 2004). However, it has also been suggested that some nest site repeatability may exist, with certain females preferring to lay closer to the high tide line and others laying far up the beach. This repeatability has not been studied in depth and, if it were found, could be used to infer evolutionary potential (Kamel & Mrosovsky 2004, Mrosovsky 2006).

The aim of this project is to determine whether individual leatherbacks nesting in Tortuguero show nest site preferences and fidelity, by analyzing subsequent nest placements and their tendency to stay on the same zone of the beach. Hatching and emergence success is also compared between subsequent nest placements, in order to examine the results of individual nest placements and determine whether or not there are “bad nesters” (Kamel & Mrosovsky 2004).

MATERIALS AND METHODS

Study site: This study was carried out at Tortuguero on the Caribbean coast of Costa Rica, in the province of Limón. The 35.6km long beach is located between the Tortuguero and Parismina rivermouths (10°35’48’’-10°19’02’’N, 83°31’28’’-83°21’23’’W). The 6km of beach closest to Parismina are separated from the remaining 29.6km by the Jalova lagoon. The beach is black sand, and backed by a canal system. It is an unstable beach, subject to erosion and strong tides and is, therefore, commonly covered by logs and other debris (Runemark 2006). For historical reasons, the beach is marked into 1/8 of a mile sections, from North to South, with the Tortuguero rivermouth originally designated as Zero (Fowler 1979). However, due to accretion cycles, the rivermouth is currently at -3/8 (N. Neeman, pers. obs). Tortuguero village is located mostly (with the exception of a few hotels and the airport) between miles 2 5/8 and 3 3/8. Tortuguero National Park starts at mile 3 3/8 and the majority of the beach is within its limits (N. Neeman, pers. obs) (Fig1).

Data collection: The field work was conducted by the author and Caribbean Conservation Corporation (CCC) Research Assistants and Field Coordinators. All the data were collected during the CCC Leatherback Program (which runs annually from March through June), following the Leatherback Program Monitoring Protocol (Nolasco *et al* 2008), and under authority of a research permit from the Ministry of Energy, Environment and Telecommunications (MINAET). Research Assistant (RA) duties were carried out by the author in 2007 and 2008; data from previous years were used with the permission of CCC. The data used herein are from 1997 to 2008, which corresponds to 12 nesting seasons.

Every night of each nesting season, the northern five miles of Tortuguero beach were patrolled by at least 2 RAs, following variable schedules (normally five hour shifts, between 8pm and 4am). Individual leatherbacks are identified by metal tags placed on their rear flippers; if no tags are found then two new ones are attached and the numbers recorded. For all leatherbacks that were encountered while the egg chamber was open the exact nest location was marked by placing three pieces of flagging tape in the vegetation and measuring the distance from each one to the centre of the egg chamber. The distance from the nest to the most recent, visible high tide line was also recorded. The zone of the nest was also noted, using one of three categories: vegetation or full shading (v), border or partial shading (b) and open or no shading (o). Marked nests were checked each morning during the incubation period to monitor their fate; any evidence that the nest had been washed out, predated or poached was recorded. Signs of hatching were also noted. Two days after hatching was reported, the nest was excavated. If no hatching was observed, excavation took place after 75 days. During excavation eggs were categorized as: empty shells (only counted if more than 50% of the shell was found in one piece), unhatched eggs, pipped eggs, and predated eggs. Any live or dead hatchlings encountered were also noted.

For the analyses, only females observed nesting more than once were considered. Nest placement was described using horizontal (along the coastline) and vertical (ocean-to-vegetation axis) distribution on the beach. For the horizontal distribution, the beach was divided into five sections, each one mile in length, giving categories 0-4 running from north to south. Category Zero also includes nests near the rivermouth and category Four includes one nest laid just past the mile 5 marker. For the vertical distribution, nests were divided into three categories, taking into account the zone and the distance to the high tide line. These categories were created in order to better reflect the use of the beach by the turtles: Zone I includes nests laid below the high tide line or up to 1m above it (due to the difficulty in determining the high tide line at night); Zone II describes nests more than 1m above the high tide line but not in the vegetation (recorded as open in the database); Zone III corresponds to nests placed either in the vegetation or on the vegetation border (recorded as either vegetation or border in the database).

Hatching and emergence success was calculated using the data collected during excavation of the nests. Nest hatching success was calculated as number of empty shells / total number of eggs. Emergence success was calculated as (number of empty shells - dead hatchlings - live hatchlings) / total number of eggs.

Statistical analyses: The pairs of subsequent observations were treated as independent observations and no distinction was made between observations from different years and those in the same year. First, chi-square tests were used to verify that nest distribution (both vertical and horizontal) was non-random. Then, in order to analyze the relationship between subsequent nesting events, contingency tables were created for the pairs of nesting events, using the previous nest site location as the column and the next location as the row. This refers to pairs of subsequent observations per female, i.e. observations 2- 3 or 3-4. One such contingency table was created for vertical zone selection and one for horizontal. These tables were tested using chi-square tests of dependence. Finally, hatching success and emergence success between previous and next nesting events were correlated (Spearman, $p < 0.05$).

RESULTS

The data obtained correspond to 94 pairs of subsequent nesting events, for 70 different females. Most females (51) were only observed twice during the study period, 15 females were seen three times, three were observed on four occasions, and one female was recorded five times (all during the 2001 nesting season). During the 2007 and 2008 seasons, 16 and 23 nests (respectively) were studied and used in the analysis.

Vertical nest zone selection was non-random, with most nests (83.5%) found in Zone 2 (X^2=186.5, $p<0.001$, df=2, Fig2). Horizontal nest site selection was also not random: more nests were laid in section 2 than any other section (X^2=13.6, p=0.009, df=4, Fig3). Nests would be expected to be scattered randomly (20% in each section) but 28.6% of nests were found in section 2. The other sections showed close to 20% of the nests each, except section 0 with 11.6%.

For subsequent nesting attempts, vertical nest zone selection was not independent (X^2=11.4, p=0.02, df=4, Table 1). The most frequent tendency (72.3% of all observed pairs) was to repeat Zone II, although Zone II was also chosen after choosing Zone I (in 12 out of 13 cases where the initial choice was Zone I) (Table 1). Horizontal nest zone selection was also not independent (X^2=26.5, p=0.048, df=16, Table 2). In this case, it was also common to repeat the selection for Section 2, although the pattern seems less pronounced than that observed for vertical zones (in only 14 of 33 pairs of nesting events were both nests laid in Section 2). There is no pronounced pattern in terms of nesting close to the first nest site (no increased frequencies along the diagonal axis of Table 2), however there is a tendency to stay within two miles of the first nesting section.

No correlation was found between hatching success of subsequent nesting events (r=0.21, p=0.09, n=70, Fig4), nor between their emergence success (r=0.19, p=0.12, n=70, Fig5).

DISCUSSION

Most nesting occurred in vertical Zone II or open sand, which is consistent with the observations of Whitmore & Dutton (1985) for Suriname, Nordmoe *et al.* (2004) for Playa Grande, Costa Rica and for Awa:la-Ya:lima:po, French Guiana (Kamel and Mrosovski 2004). These studies found a strong preference (approximately 80-90%) for open sand nest sites in leatherback turtles. This preference for nests in the middle section of the beach is consistent with the idea of balancing the negative consequences of laying too close to the water with those of laying too close to the vegetation and suggests that optimal humidity and temperature are found in this area (Caut *et al*. 2006, Katilimis *et al.* 2006, Mrosovsky 2006, Runemark 2006).

As for nesting distribution along the coastline, most nests were found in Section 2 (between miles two and three), which is the section that has the most development and artificial lights. This conflicts with the finding of Nordmoe *et al.* (2004), who found reduced nesting on the more developed parts of Playa Grande and attributed this to increased artificial lighting. For Tortuguero, most lights visible on the beach come from the village and small hotels between mile markers 2 2/8 and 3 3/8 (Nolasco *et al.* 2008), so it is interesting that there was increased nesting recorded in this section. More research (for instance, comparison of these results with those of track surveys conducted in the morning) is needed to determine if this is a real trend or an artifice created by the patrolling system that the CCC uses. It is possible that more nests were observed in this area because it is the closest to the CCC station (located in mile 2 5/8) and the protocol for leatherback season is to wait for a turtle to complete nesting. This sometimes means waiting if the turtle is first observed emerging from the sea, which may bias the data with respect to where nests are marked. If a real preference exists in the Tortuguero population towards artificially lighted areas, this would merit further research into the reasons for this behavior. Such a pattern has not been described for leatherback turtles, although it has been suggested for other species such as the olive ridley (F. Bolaños, pers comm). Artificial lights cause hatchlings to become disoriented and often move into the vegetation rather than the ocean (Whitmore & Dutton 1985, Kamel & Mrosovsky 2004). Thus, a preference for nesting in these areas would be a sign of a poorly adapted population and would suggest further measures should be taken against artificial lights on the beach.

Both horizontal and vertical nest site selection were not independent for subsequent nesting events, which may be due to the overall population tendency to choose Zone II and Section 2 (vertical and horizontal, respectively). It is clear when looking at the contingency tables that they are skewed towards the most common nest site preference at a population level (females nesting in vertical and horizontal zone 2, for both nesting events). It is also clear that females that have selected a nesting site at risk of being washed out (vertical Zone I) do not tend to repeat this selection; this happened in only one of 13 pairs of nesting events (Table 1). Also, there is no tendency to nest close (same mile) to the first nest site selection, showing no evidence for repeatability. The tendency to nest within 2 miles of the initial choice merits further study to determine whether it is a real trend for the species or due to incomplete data. A similar tendency was found by Nordmoe *et al.* (2004) for Playa Grande, who determined this was not a real nest site preference but simply a repetition of the initial nest site, regardless of where this first choice was located. Therefore, it is difficult to determine whether the pattern found corresponds to real, repeated preference at an individual level or is simply a reflection of the general population preference.

No correlation was found between either hatching or nesting success for subsequent nesting events. From the results, it appears that individual nest site selection does not play an important role in determining nest success. It is more likely that it is influenced at a population level, either by behavioral or environmental factors. To investigate further the concept of nest site selection it would be interesting to analyze nesting preferences for individual females on different nesting beaches and throughout different nesting seasons; such a study would hopefully yield clearer and more reliable results, due to a larger and more complete data set for each female. A regional database, allowing comparison between different beaches, would help to better determine the role that individual nest site selection plays in the overall patterns observed for the population. This knowledge would allow for standardization of conservation practices currently in place under different organizations at different beaches. For instance, some researchers working at protected nesting beaches on the Caribbean coast of Costa Rica include nest relocation in their protocol. If nest location choices are repeated by females, then relocating doomed nests may distort the gene pool by selecting for “bad nesters” (Mrosovsky 2006). If they are not, then this danger is not significant and, along with other control measures and proper protocol, it would be recommended that nest relocation be considered as a conservation measure for Tortuguero beach.

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Resumen: La selección de sitio de anidación por parte de hembras individuales de la tortuga baula, *Dermochelys coriacea*, es tema de disputa. Algunos autores sugieren que una hembra dispersa sus nidos al azar para maximizar su éxito en las inestables playas que elige para anidar mientras que otros sugieren que existe cierta fidelidad al sitio de anidación. Se estudió la selección de sitios subsecuentes de anidación y sus éxitos de eclosión y emergencia para playa Tortuguero 1997-2008 (datos recolectados por la Caribbean Conservation Corporation). Se crearon tablas de contingencia para las selecciones subsecuentes de sitios de anidación, usando el sitio previo como columna y el siguiente como fila, esto tanto para selección horizontal como vertical. Además los éxitos de eclosión y emergencia entre el sitio previo y siguiente se correlacionaron. A lo largo del eje océano-vegetación, se encontró una preferencia por la zona II o arena abierta (X^2=11.4, p=0.02, gL=4). A lo largo de la costa, se prefirió la Sección 2, entre los marcadores de milla 2 y 3 (X^2=26.5, p=0.048, gL=16). No se encontró correlación entre los éxitos de eclosión de anidaciones subsecuentes (r=0.21, p=0.09, n=70), ni entre sus éxitos de emergencia (r=0.19, p=0.12, n=70). En general, la prefencia individual por sitios de anidación corresponde con la que se encuentra a nivel poblacional; una preferencia por zonas de arena abierta, principalmente en la sección media de la playa. La selección de sitios de anidación en zonas bajo riesgo de ser lavadas por la marea no se repitió en la siguiente anidación. Dado esto, y el hecho que no existe correlación entre los éxitos de anidaciones subsecuentes, no existen pruebas claras que la selección individual juegue un papel importante en la preferencia general de sitio de esta especie en Tortuguero. Más investigación, incluyendo datos para una misma hembra en diferentes playas hará que este tema se aclare. La cooperación y la union de datos entre las organizaciones que patrullan las diferentes playas facilitará estudios a futuro.

Palabras clave: baula, *Dermochelys coriacea*, patrones individuales de anidación, distribución de nidos, selección del sitio de anidación.

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TABLE 1

Contingency table showing subsequent vertical zone selections (on the ocean-to-vegetation axis) by individual leatherback females, Dermochelys coriacea, *Tortuguero, Costa Rica, 1997-2008. For description of zones, see Materials and Methods.*

Previous Zone/ Next Zone	I	II	III	**Total**
I	1	4	0	**5**
II	12	68	2	**82**
III	0	5	2	**7**
Total	**13**	**77**	**4**	**94**

TABLE 2

Contingency table showing subsequent horizontal zone selections (along the coastline) by individual leatherback females, Dermochelys coriacea, *Tortuguero, Costa Rica, 1997-2008.*

Previous Section/ Next Section	0	1	2	3	4	**Total**
0	2	2	1	0	1	**6**
1	3	4	1	0	4	**12**
2	5	3	14	8	3	**33**
3	1	3	8	4	8	**24**
4	2	3	2	6	6	**19**
Total	**13**	**15**	**26**	**18**	**22**	**94**

Note: Sections correspond to the mile in which the nest was laid (e.g. section 1 is between miles 1 and 2).

FIGURE LEGENDS

Fig. 1. Map of study site, Tortuguero, Costa Rica.

Fig. 2. Vertical zones (on the ocean-to-vegetation axis) selected for nesting by the leatherback sea turtle, *Dermochelys coriacea*, at Tortuguero, Costa Rica, 1997-2008.

Fig. 3. Horizontal sections (along the coastline) selected for nesting by the leatherback sea turtle, *Dermochelys coriacea*, at Tortuguero, Costa Rica, 1997-2008.

Fig. 4. Relationship between hatching success of subsequent nesting events in the leatherback sea turtle *Dermochelys coriacea*, at Tortuguero, Costa Rica, 1997-2008.

Fig. 5. Relationship between emergence success of subsequent nesting events in the leatherback sea turtle, *Dermochelys coriacea*, at Tortuguero, Costa Rica, 1997-2008.

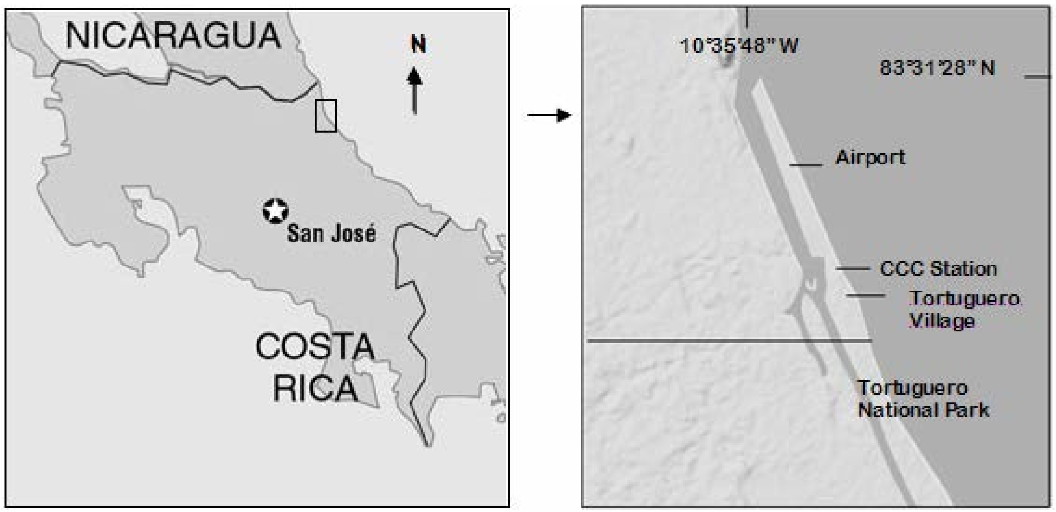
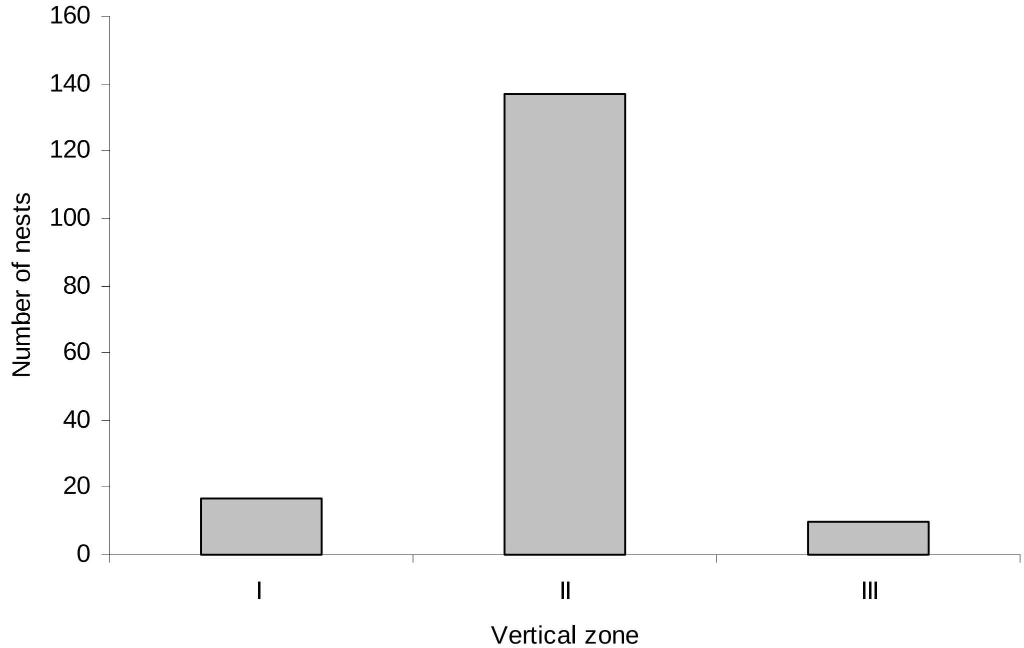

NICARAGUA
N
San José
COSTA
RICA
10°35'48" W
83°31'28" N
Airport
CCC Station
Tortuguero
Village
Tortuguero
National Park

Figure 1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140
120
100
80
60
40
20
0
Number of nests
I
II
III
Vertical zone

Figure 2

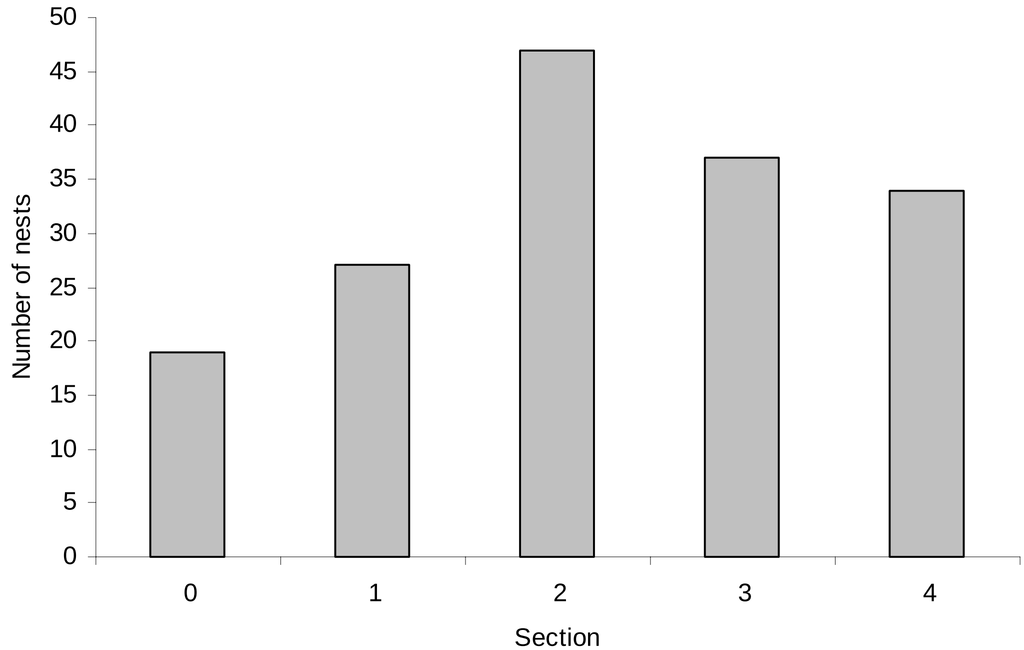
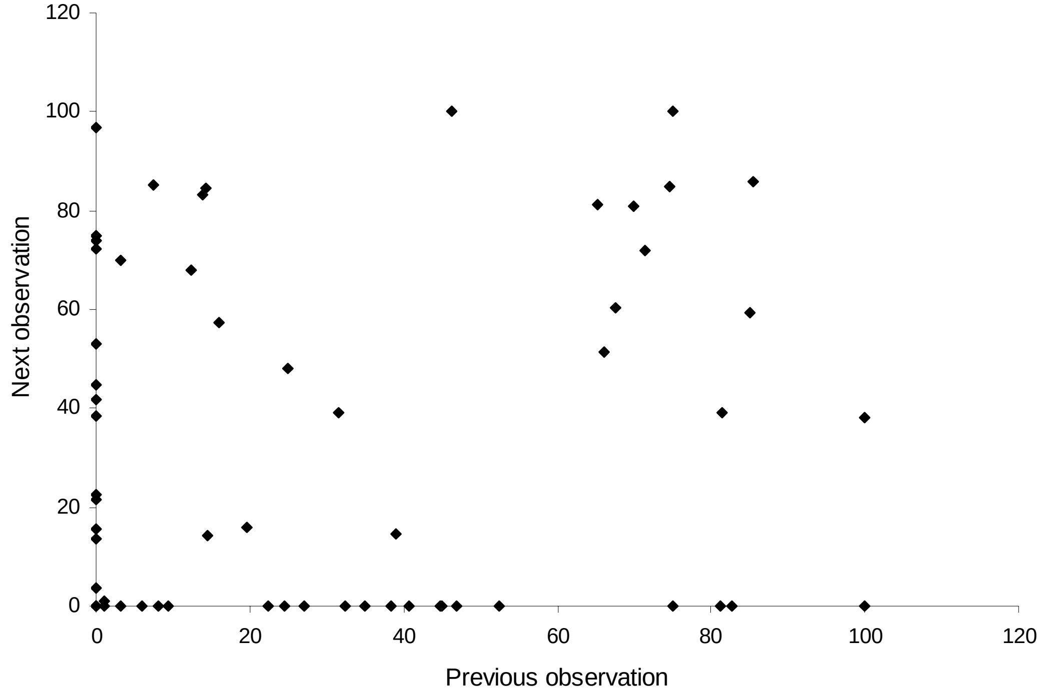


Figure 3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100
80
60
40
20
0
Next observation
0
20
40
60
80
100
120
Previous observation

Figure 4

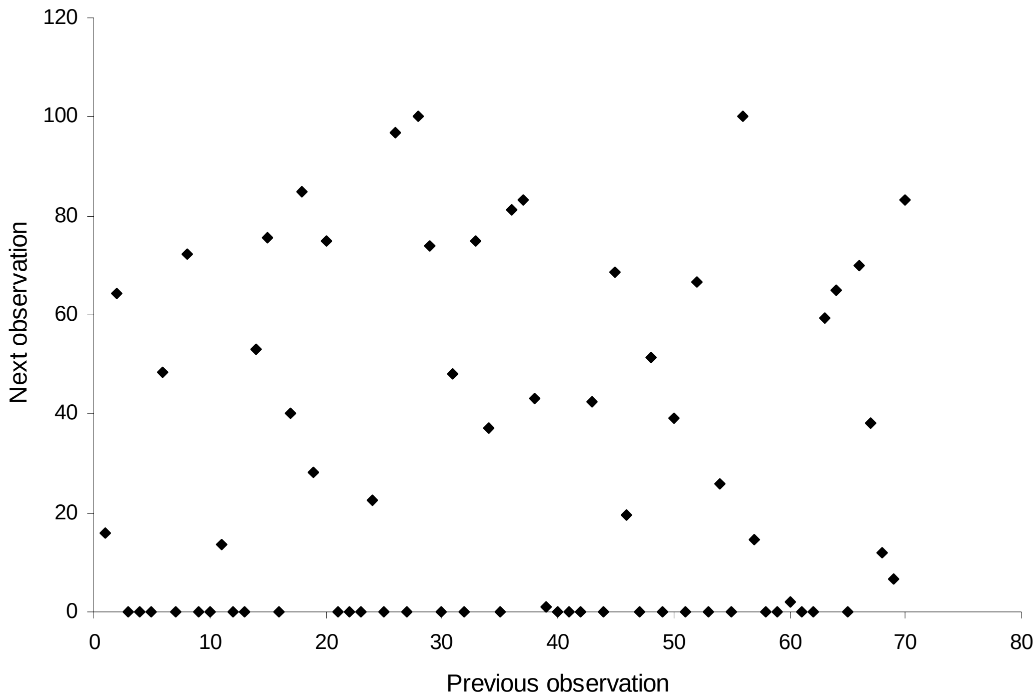
120
100
80
60
40
20
0
Next observation
0
10
20
30
40
50
60
70
80
Previous observation

Figure 5